



## Aglaopheniid hydroids (Cnidaria: Hydrozoa: Aglaopheniidae) from bathyal waters of the Flemish Cap, Flemish Pass, and Grand Banks of Newfoundland (NW Atlantic)

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### Abstract

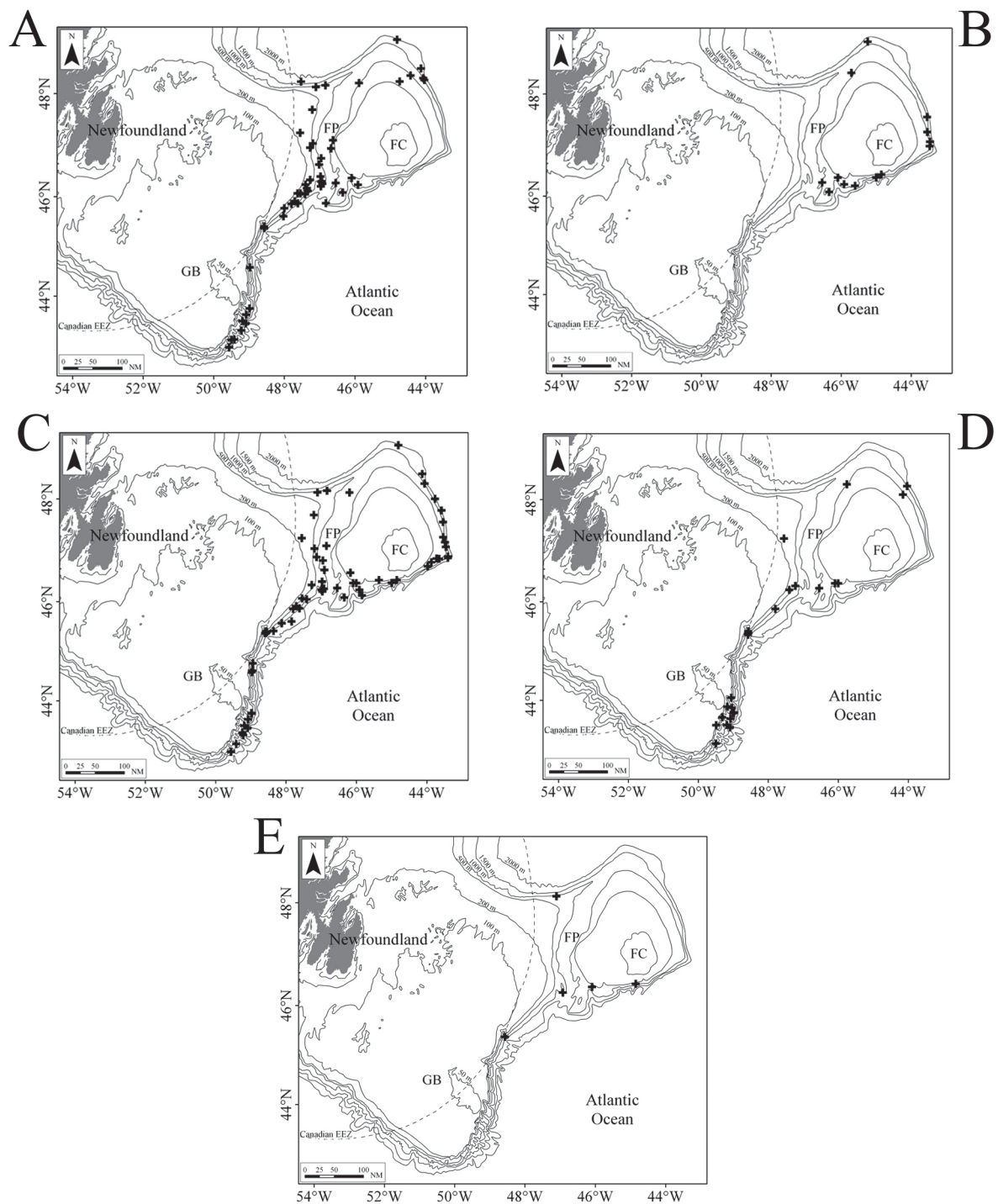
Five species of aglaopheniid hydroids (*Aglaophenopsis cornuta*, *Cladocarpus diana*, *C. formosus*, *C. integer*, and *Nematocarpus ramuliferus*) were collected from the Flemish Cap, Flemish Pass, and Grand Banks of Newfoundland during surveys with bottom trawls, rock dredges, and scallop gear. All are infrequently reported species, with *C. diana* being discovered for the first time since its original description from Iceland. We document here the southernmost collections of *C. diana* and *N. ramuliferus*, both previously unknown in the western Atlantic. Each of the five species is described and illustrated based on fertile material, a key is provided for their identification, and bathymetric distributions are noted. Known depth ranges are extended for *A. cornuta*, *C. diana*, and *C. integer*. *Aglaophenopsis* and *Nematocarpus* are recognized as genera distinct from the polyphyletic *Cladocarpus*, based on the unique structure of the phylactocarp in the former, and the existence of appendages with nematothecae (ramuli) on almost all thecate internodes of hydrocladia in the latter. These appendages occur even in the absence of gonothecae, and are here considered defensive structures that protect the hydranths. In differing from typical phylactocarps, we accept the contention that they are characters of generic value.

**Key words:** *Aglaophenopsis*, *Cladocarpus*, *Nematocarpus*, deep-sea, northwestern Atlantic

### Introduction

The hydrozoan family Aglaopheniidae Marktanner-Turneretscher, 1890 is a speciose taxon comprising around 248 valid species worldwide (see Bouillon *et al.* 2006). Division of genera within the group is based mainly on the gonosome, because reliable differential characters are lacking in the trophosome (Leloup 1932). Aglaopheniids have been reported infrequently in the western Atlantic northwards of the 40°N parallel, and especially so in waters off the east coast of Canada.

While the hydroid fauna of shallow waters off the Atlantic coast of Canada is relatively well known (Fraser 1944), that of deeper neritic and bathyal waters has received little attention and is consequently poorly known. At such depths off Newfoundland, only two species of aglaopheniids have been recorded previously. *Aglaophenopsis cornuta* (Verrill, 1879) was reported from two locations north of the island (53°34'N–52°01'W, ca. 1792 m; 52°25'N–52°12'W, ca. 296 m) by Jäderholm (1919: 11), while *A. cornuta* and *Cladocarpus integer* (G.O. Sars, 1874) were found in collections from a station to the northeast of Newfoundland (51°22'30"N–50°31'30"W, 457 m) by Calder (1970: 1540). Two other aglaopheniid species penetrating into bathyal waters, *Lytocarpia myriophyllum* (Linnaeus, 1758) and *Cladocarpus formosus* Allman, 1874, range both north and south of Newfoundland along the North American Atlantic coast (Fraser 1944, 1946) but have yet to be reported from that locale.



**FIGURE 1.** Distribution of the five aglaopheniid species in the study area. A) *Aglaophenopsis cornuta* (Verrill, 1879). B) *Cladocarpus diana* Broch, 1918. C) *Cladocarpus formosus* Allman, 1874. D) *Cladocarpus integer* (G.O. Sars, 1874). E) *Nematocarpus ramuliferus* (Allman, 1874). FC, Flemish Cap; FP, Flemish Pass; GB, Grand Banks.

In a literature review, we found records of only eight species of aglaopheniids, referable to the genera *Aglaophenopsis* Fewkes, 1881, *Cladocarpus* Allman, 1874, and *Lytocarpia* Kirchenpauer, 1872, in the region between 40°N (New York Bight east of New Jersey) and Baffin Bay (including the west coast of Greenland) (Table 1). Some have been recorded only a few times and appear to be quite rare, while another is probably not valid. Scarcity of aglaopheniids in the northwestern North Atlantic may be attributed in part to the fact that they are predominantly a warm-water group (Calder 1997a: 40).

**TABLE 1.** Hydroids of family Aglaopheniidae recorded in the western Atlantic from 40°N (New York Bight) to Baffin Bay, including western and southwestern Greenland, incorporating species discussed in the present report. \*) Distributions refer to this region of the western North Atlantic only.

Species	Present taxonomic status	Phylactocarp	Distribution*
<i>Aglaophenopsis compressa</i> (Bonnievie, 1899)	<i>Aglaophenopsis bonnievieae</i> (Jäderholm, 1909)	Alternately branched phylactocarp with hydrothecae	SW Greenland
<i>Aglaophenopsis cornuta</i> (Verrill, 1879)	Accepted	Forked (Y-shaped) phylactocarp with terminal hydrothecae, arising laterally between mesial nematotheca and hydrothecal base. Phylactocarp may be absent in fertile colonies	Canada, USA
<i>Aglaophenopsis verrilli</i> Nutting, 1900	Accepted	Forked (Y-shaped) phylactocarp originating laterally between mesial nematotheca and hydrothecal base	USA
<i>Cladocarpus campanulatus</i> Ritchie, 1912	Accepted	Gonothecae unprotected or protected by a small unbranched phylactocarp	SW Greenland
<i>Cladocarpus crenatus</i> (Fewkes, 1881)	Doubtful, probably <i>Cladocarpus formosus</i>	Unknown	USA
<i>Cladocarpus diana</i> Broch, 1918	Accepted	Antler-shaped phylactocarp arising laterally near hydrothecal base, with unpaired nematothecae	E of Canada (new record)
<i>Cladocarpus flexilis</i> Verrill, 1885	Accepted	Antler-shaped phylactocarp arising between mesial nematotheca and hydrothecal base	USA
<i>Cladocarpus formosus</i> Allman, 1874	Accepted	Antler-shaped phylactocarp with opposite paired nematothecae, arising between mesial nematotheca and hydrothecal base. Phylactocarp may be absent in fertile colonies.	Canada, USA
<i>Cladocarpus integer</i> (G.O. Sars, 1874)	Accepted	Non-ramified phylactocarp arising between mesial nematotheca and hydrothecal base. Phylactocarp may be absent in fertile colonies	Canada, USA
<i>Cladocarpus pourtalesii</i> Verrill, 1879	<i>Cladocarpus integer</i>	See <i>Cladocarpus integer</i>	Canada, USA
<i>Cladocarpus speciosus</i> Verrill, 1879	<i>Cladocarpus formosus</i>	See <i>Cladocarpus formosus</i>	Canada, USA
<i>Lylocarpia myriophyllum</i> (L., 1758)	Accepted	An open corbula with nematothecae and hydrothecae formed by modified hydrocladia	Canada, USA
<i>Nematocarpus ramuliferus</i> (Allman, 1874)	Accepted	Gonothecae not clearly protected. Strongly septate appendage (ramuli) arising between mesial nematotheca and hydrothecal base occurring putatively on all thecate internodes of hydrocladia, sometimes ramified, and without gonothecae. Appendages sometimes with hydrothecae	E of Canada (new record)

According to the generic diagnoses of aglaopheniids in Bouillon (1985) and Bouillon *et al.* (2006), all species of the family known to occur between Baffin Bay and the Maritime Provinces of Canada are referable to *Cladocarpus*, with the exception of *Lytocarpia myriophyllum*. *Cladocarpus* was originally established by Allman (1874) to accommodate *C. formosus*, a species first described from the Faroe-Shetland Channel in the northeastern North Atlantic. Its primary distinguishing characters, according to Allman, were differences in morphology of the reproductive structures: gonothecae were solitary and protected by phylactocarps ('gonangia not included in corbulae') arising as appendages of an unmodified hydrocladium. Bouillon *et al.* (2006) listed 66 species of *Cladocarpus* worldwide, most of them from deep-water. However, the genus has essentially become a collective group, and a revision is needed. Some genera merged with it appear distinctive in characters of their phylactocarps and, in our opinion, are valid (see also Ramil & Vervoort 1992). One of these is *Aglaophenopsis*, with several representatives in the western North Atlantic. Fraser (1944) included four species in that genus from the Atlantic coast of North America, with three of them being seldom recorded and poorly known.

During 2006–2010, the Spanish Institute of Oceanography, in collaboration with several other institutions, carried out a number of research surveys on the Flemish Cap, the Flemish Pass, and the “tail” and “nose” of the Grand Banks of Newfoundland (Figure 1). Abundant material of sessile benthic fauna was collected over a wide range of depths, mainly in the bathyal zone (see Murillo *et al.* 2011). Hydroids comprise a significant part of those catches, and numerous colonies of aglaopheniids referable to five species were collected. All five are described and illustrated in this paper. Two of them are rare and previously unknown in the western Atlantic, one of which is reported for the first time since its original description. The generic value of certain gonosomal characters is discussed, with special emphasis on the genera *Aglaophenopsis* and *Nematocarpus* Broch, 1918.

## Material and methods

Material examined during this study came from two research programs. Part was obtained during groundfish bottom trawl surveys carried out by the Spanish Institute of Oceanography (Instituto Español de Oceanografía, IEO) and the European Union (EU) on board the Spanish R/V “Vizconde de Eza”. The remainder came from rock dredge and scallop gear samples taken by the Spanish R/V “Miguel Oliver,” operated by the Spanish General Secretariat of the Sea (Secretaría General del Mar) under the NEREIDA project. Groundfish bottom trawl surveys covered the “tail” of the Grand Banks of Newfoundland between 40 and 1500 m, the Flemish Cap between 130 and 1450 m, and the Flemish Pass between 110 and 1450 m. These surveys were carried out annually between spring and summer using a random stratified sampling design with standardized 30-min tows and vessel speed of three knots. Campelen 1800 bottom trawl gear was used in the Flemish Pass and the Grand Banks of Newfoundland, whereas Lofoten bottom trawl gear was used at Flemish Cap. NEREIDA surveys were undertaken in the Flemish Pass, Flemish Cap, and slope of the Grand Banks of Newfoundland at depths between 700 and 2000 m. These surveys were carried out during spring and summer using a rock dredge and scallop gear. Tows of 15-min were made at a vessel speed of about 1.5 knots. NEREIDA is a multidisciplinary research project involving scientists from Instituto Español de Oceanografía (IEO), Fisheries and Oceans Canada (DFO), Natural Resources Canada (NRCAN), Centre for the Environment, Fisheries and Aquaculture Science (Cefas), Instituto de Investigaciones Marinas (CSIC), Secretaría General del Mar (SGM), Polar Research Institute of Marine Fisheries and Oceanography (PINRO), and the P.P. Shirshov Institute of Oceanology (RAS). Our study is based on material from groundfish bottom trawl surveys undertaken on the “tail” of the Grand Banks and Flemish Cap during 2007 and on the “nose” of the Grand Banks and Flemish Pass from 2006–2010, as well as from NEREIDA surveys during 2009 and 2010.

Samples were fixed on board in 70 % ethanol. Voucher material of each species has been deposited in collections of the Invertebrate Zoology Section, Department of Natural History, Royal Ontario Museum (Canada), the Oceanographic Center of Vigo (IEO, Spain), and the Okendo Museum, Donostia-San Sebastián (Spain).

Depths in Levinsen (1893) and Broch (1918) were given in Danish fathoms (*favn*), equivalent to 1.883 m. Fathoms in other papers have been taken to equal 1.828 m.



**TABLE 2.** Species of aglaopheniid hydroids reported from the western North Atlantic between 40°N (New York Bight) and Baffin Bay (including western and southwestern Greenland) but not recorded during the present study. Literature records are not intended to be exhaustive.

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*Aglaophenopsis bonnevieae* (Jäderholm, 1909): 60°16'5N–47°48'W and 60°22'N–47°27'W (southwest Greenland, 135 m and 120 m) [Kramp 1932a, as *Aglaophenopsis compressa* (Bonnevie, 1899)]. No further records in the western Atlantic.

*Aglaophenopsis verrilli* Nutting, 1900: 40°34'N–66°04'W (off Georges Bank, 3184 m) [Nutting (1900) and Fraser (1944)] = *Cladocarpus verrilli* in Bouillon *et al.* (2006) and Schuchert (2012b).

*Cladocarpus campanulatus* Ritchie, 1912: 60°22'N–47°27'W (southwest Greenland, 120 m) (Kramp 1932a). No further records in the western Atlantic.

*Cladocarpus crenatus* (Fewkes, 1881): 41°25'N–65°35'W (2270 m) [Fewkes (1881), as *Aglaophenia crenata*], Nutting (1900) as *Aglaophenia* ? *crenata* referring to Fewkes (1881), east of Nantucket (Fraser 1944), referring to Fewkes (1881), as *Cladocarpus* ? *crenatus* with unknown gonosome. Likely coterminous with *Cladocarpus formosus*.

*Cladocarpus flexilis* Verrill, 1885: southern coast of New England (Verrill 1885), seven stations in the Georges Bank area at different depths (*Fish Hawk* and *Albatross* stations) (Nutting 1900), Martha's Vineyard and several stations in the Georges Bank area (Fraser 1944, some stations referring to Nutting 1900).

*Lytocarpia myriophyllum* (L., 1758): Massachusetts Bay, Mingan Islands (Quebec), Eastport, Maine (A. Agassiz 1865 as *Sertularia myriophyllum*; Whiteaves 1901 and Fraser 1918 as *Thecocarpus myriophyllum*), 41°44'N–64°36'W (Le Have Bank, Nova Scotia, ca. 110 m) (Smith & Harger 1874 as *Aglaophenia myriophyllum*; Whiteaves 1901 and Fraser 1918 as *T. myriophyllum*), off Cape Gaspé (Gulf of St. Lawrence, Quebec, ca. 55 m) (Whiteaves 1901 and Fraser 1918 as *T. myriophyllum*), eastern Canada [(Kindle & Whittaker 1917, ca. 55–110 m, as *T. myriophyllum*, based on literature records)].

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## Results

### Class Hydrozoa Owen, 1843

#### Subclass Leptolina Haeckel, 1879

#### Order Leptothecata Cornelius, 1992

#### Suborder Conica Broch, 1910

#### Family Aglaopheniidae Marktanner-Turneretscher, 1890

##### *Aglaophenopsis cornuta* (Verrill, 1879)

(Figs. 1A, 2A–G, tables 1, 3, 9–12)

*Cladocarpus cornutus* Verrill, 1879: 310.—Levinsen 1893: 208, pl. 8, fig. 19–22.—Vanhöffen 1897: 246.—Jäderholm 1909: 110.—Kramp 1913: 28.—Kramp 1914: 1059.—Fraser 1946: 417.—Calder 1970: 1540, pl. 8, fig. 7.—Peña Cantero & García Carrascosa 1999: 214.—Schuchert 2001: 137, fig. 117A–E.—Bouillon *et al.* 2006: 283.

*Aglaophenia cornutus*: Bonnevie 1899: 94.

*Aglaophenopsis cornuta*: Nutting 1900: 120, pl. 30, fig. 6–9.—Whiteaves 1901: 28.—Broch 1910: 234.—Kindle & Whittaker 1917: 232.—Broch 1918: 77, fig. 39a–b, fig. 40a–d, fig. 41.—Jäderholm 1919: 11.—Fraser 1921: 177, fig. 102.—Kramp 1932a: 56.—Kramp 1932b: 20.—Kramp 1943: 44.—Fraser 1944: 395, pl. 85, fig. 382.—Vervoort 1972: 204.—Calder 1997b: 88.—Henry 2001: 163.

**Material examined.** FN3L06 L51, 2 fertile colonies, largest one 9.5 cm high; FN3L06 L85, one fertile colony 7.0 cm high; FN3L06 L88, one fertile colony 10.5 cm high; FN3L06 L92, one fertile colony 15.0 cm high; PLA07 L61, one sterile colony 8.4 cm high; PLA07 L99, one sterile colony 10.0 cm high; PLA07 L107, one fertile colony 6 cm high; FC07 L74, one sterile colony 7.2 cm high; FC07 L133, one sterile colony 4.3 cm high; FC07 L153, one sterile colony 13.0 cm high; FC07 L171, one sterile fragment 1.6 cm high; FC07 L177, one sterile colony 5.5 cm

high; FC07 L178, one fertile fragment 6.2 cm high; FN3L08 L88, 3 fertile colonies, largest one 21.0 cm high; FN3L08 L89, 3 fertile colonies, largest one 15.0 cm high; FN3L09 L80, one fertile colony 10.0 cm high; FN3L09 L89, one fertile colony 16.0 cm high; FN3L10 L35, one fertile colony 14.0 cm high; FN3L10 L57, one fertile colony 9.0 cm high; FN3L10 L87, one fertile colony 15.5 cm high; NEREIDA0509 RD4, one fertile colony 12.2 cm high; NEREIDA0509 RD6, 5 colonies, largest one 15.3 cm high, 2 of them fertile; NEREIDA0509 RD7, 6 colonies, up to 15.6 cm high, some fertile; NEREIDA0609 RD26, 2 sterile colonies, largest one 4.2 cm high; NEREIDA0609 RD27, 3 colonies, largest one 5.5 cm high, one fertile; NEREIDA0609 RD28, 2 fertile colonies, both 6.0 cm high; NEREIDA0609 RD41, 34 colonies, up to 11.3 cm high, some fertile; NEREIDA0709 RD49, 5 colonies, largest one 6 cm high, 2 fertile; NEREIDA0709 RD59, 2 fertile colonies, largest one 9.5 cm high; NEREIDA0709 RD60, one sterile colony 5.2 cm high; NEREIDA0610 RD62, one sterile colony 2.0 cm high; NEREIDA0610 RD67, one fertile colony 3.0 cm high; NEREIDA0610 RD71, one sterile fragment 2.2 cm high; NEREIDA0610 RD74, 23 colonies, up to 10.3 cm high, some fertile; NEREIDA0710 RD75, one sterile colony 6.0 cm high; NEREIDA0710 RD76, one fertile colony 8.7 cm high; NEREIDA0710 RD77, 2 sterile colonies, largest one 5.7 cm high; NEREIDA0710 RD78, one sterile colony 3.0 cm high; NEREIDA0710 RD79, one fertile colony 10.2 cm high; NEREIDA0710 RD80, 8 colonies, up to 8.4 cm high, some fertile; NEREIDA0710 RD87, one fertile colony 12.0 cm high; NEREIDA0710 RD88, 3 colonies, largest one 6.6 cm high, 2 fertile; NEREIDA0710 RD92, 2 sterile colonies, largest one 8.4 cm high; NEREIDA0810 RD97, 5 colonies, largest one 8.0 cm high, 3 fertile; NEREIDA0810 RD98, 4 colonies, largest one 8.4 cm high, one fertile; NEREIDA0810 RD99, 13 colonies, up to 8.5 cm high, some fertile; NEREIDA0810 RD100, 3 sterile colonies, largest one 9.0 cm high; NEREIDA0810 RD101, one sterile colony 9.1 cm high; NEREIDA0810 RD102, 2 colonies, largest one 7.8 cm high, one fertile; NEREIDA0810 RD103, 9 colonies, up to 18 cm high, some fertile; NEREIDA0810 RD104, 15 colonies, up to 28.7 cm high, some fertile.

**Description.** Colonies up to 28.7 cm high, formed by a broad hydrorhizal mass supporting a polysiphonic stem, up to 3.0 mm wide proximally, thinning out to monosiphonic distally. Stem rigid, thick, erect. Ramification in one plane, profuse, up to the fourth order. Branches almost opposite, arising at slightly acute angles, long, polysiphonic for most of their length, slightly tapering distally. Stem deep brown basally and light brown distally; branches also light brown.

Main axial tube on front of stem and branches, divided into short internodes, 550–600  $\mu$ m long. Successive internodes each with one apophysis alternately right and left, giving rise to branches and hydrocladia. Three nematothecae surrounding the apophyses: one basal and two distal. Accessory tubes numerous, with neither hydrothecae nor nematothecae.

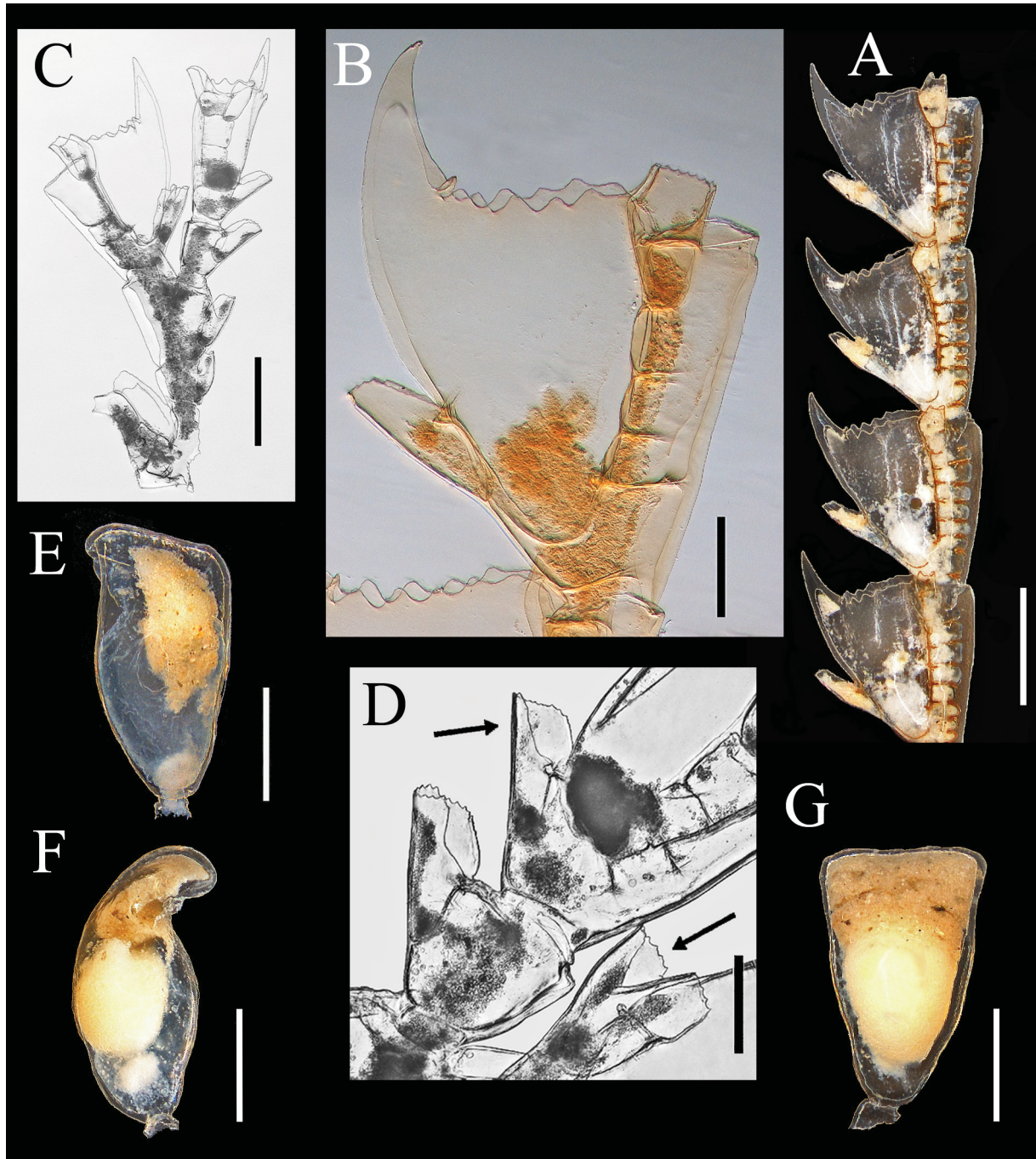
Hydrocladia alternate, up to 1.2 cm long, divided into up to 15 thecate internodes by more or less well-marked transverse nodes. Internodes with 2–9 internal septa, one hydrotheca, and three one-chambered nematothecae. Hydrotheca as long as the internode, large, conical in lateral view and somewhat oval to round in cross-section, with depth/width at rim = 1.08–1.48 ( $n = 25$ ). Intrathecal septum inconspicuous, very small, arising from the adaxial wall of hydrotheca and projecting forwards in its lumen. A characteristic abcauline median keel with a sharp, hollow tip, arising above mesial nematotheca; strong, large, laterally compressed, slightly curved, extending 332–528  $\mu$ m beyond level of hydrothecal margin, reaching end of mesial nematotheca of the following distal internode, or nearly so. Hydrothecal rim with 9–11 low cusps, including a small mesial tooth aligned with the keel.

Mesial nematothecae extending for 1/3–1/2 the length of abaxial hydrothecal wall, slightly tapering distally, with wide aperture and crenulated rim, as well as a thickening of perisarc at its basis in the axil between the wall of the hydrotheca and the nematotheca; on first internode it is slightly displaced to one side. Lateral nematothecae arising from hydrocladium, partially attached to distal hydrothecal wall, with end slightly surpassing hydrothecal rim and crenulated margin.

Phylactocarps forked (Y-shaped), segmented, up to 2.3 mm long, arising laterally from hydrothecal bases of proximal thecate internodes beside mesial nematotheca; not replacing nematotheca. Internal septa numerous. Segments short, carrying unpaired nematothecae with margin of aperture finely crenulated. Both branches with one terminal hydrotheca. Gonothecae borne on short pedicels, obovate, curved, arising singly from apophyses of stem and branches; aperture broadly oval to almost circular, latero-distal. Sex could not be ascertained.

**Remarks.** This species is readily distinguished from others in the study area by the characteristic shape of its hydrothecae (Figure 2A–C). Especially noteworthy is the presence of a pronounced median hydrothecal keel with thickened perisarc. Its tip normally reaches the base of the mesial nematotheca of the following internode, and sometimes also approaches its end. The variability of this keel was discussed by Broch (1918). *Aglaophenopsis*

*bonnevieae* (Jäderholm, 1909), sometimes sympatric with *A. cornuta* in Greenland and subarctic waters of the northwestern Atlantic (see Kramp 1932a; Schuchert 2001), likewise has a prominent, although somewhat less developed, hydrothecal keel. Moreover, its hydrotheca differs from that of *A. cornuta* in having a conspicuous intrathecal septum, and the hydrothecal rim is slightly crenulated rather than cusped. Paired nematothecae on the internodes of the main axial tube also occur in the upper axil of the apophyses rather than at its sides. Phylactocarps of *A. bonnevieae* also differ in being much more ramified and in having more hydrothecae.



**FIGURE 2.** *Aglaophenopsis cornuta* (Verrill, 1879). A) Detail of a hydrocladium, including distalmost thecate internode. B) Hydrotheca. C) Phylactocarp; note the two distal hydrothecae, one on each branch. D) Detail of a phylactocarp showing mesial nematothecae adjacent to hydrothecae (arrows); one of them is double. E–G) Gonothecae, one of them (F) in lateral view showing curvature. Scale bar: A, C, E–G= 500  $\mu$ m; B, D= 200  $\mu$ m. A, E–G= NEREIDA0810 RD104; B= PLA07 L99; C, D= NEREIDA0710 RD79.



**TABLE 3.** *Aglaophenopsis cornuta* (Verrill, 1879). Measurements (in  $\mu\text{m}$ ) of colonies from different locations and sources.

	PLA07 L99	NEREIDA0810 RD104	Schuchert (2001)
Colony			
Height (mm)	100	150	70
Hydrocladia			
Length of internode	752–900	810–923	---
Diameter at node	181–239	250–257	---
Hydrothecae			
Depth	703–794	834–860	500
Diameter at rim	380–416	380–426	300–400
Diameter at rim including the mesial tooth	550–616	588–600	---
Nematothecae			
Length of laterals	283–297	301–316	---
Diameter at level of terminal aperture	92–164	86–92	---
Length of mesial	328–378	294–340	---
Diameter of terminal aperture	62–70	65–70	---
Gonothecae			
Length	---	1200–1328	---
Maximal diameter in frontal view	---	512–606	---

Hydrothecae of *A. cornuta* somewhat resemble certain species of *Gymnangium* Hincks, 1874, including the European *G. montagui* (Billard, 1912) and others from South Africa (see Millard 1975). However, the ‘horn’ in such species of *Gymnangium* is a hypertrophied mesial nematotheca, while that of *A. cornuta* is a large median hydrothecal keel arising distal to the mesial nematotheca. The keel does not represent a highly modified median abcaulinar cusp of the hydrothecal margin because that cusp is both present and small.

The margin of the median inferior nematotheca of the thecate internodes (and also of the terminal hydrothecae of the phylactocarp), is at times deeply indented in the middle, giving the impression of a twin theca (NEREIDA0710 RD79, Figure 2D).

Colonies with gonothecae on stem apophyses, unprotected by any phylactocarps, were found in samples from some stations (NEREIDA0709 RD49).

Although originally assigned to *Cladocarpus*, this species has also been referred to *Aglaophenopsis* by several authors. According to Fraser (1944), phylactocarps of this species represent a modified mesial nematophore. In our material, however, the phylactocarp arises laterally from the base of a hydrotheca borne on a proximal thecate internode. It is situated beside a clearly distinct mesial nematotheca and does not replace it. Moreover, contrary to Fraser, both branches of the phylactocarp bear a terminal hydrotheca. The species was assigned to *Cladocarpus* (as *C. cornutus*) by both Bouillon *et al.* (2006) and Schuchert (2012a).

**Observed depth range:** 240–1885 m. The known maximum depth for the species is extended from 1200 m (Kramp 1932a) to 1885 m. A neritic-bathyal species (Calder 1997b).

**Fertile material.** Collected in August 2006 (240–1233 m depth), June and July 2007 (460–878 m depth), August 2008 (392–1198 m depth), from May to August 2009 (425–1885 m depth), and from June to August 2010 (345–1353 m depth).

**Distribution.** A North Atlantic species known from Denmark Strait (Broch 1918, ca. 253–603 m; Schuchert 2001, 200–700 m), eastern Greenland (Broch 1918, ca. 260–621), southwest Greenland at 63°36'N–55°15'W (1200 m) and 60°16'N–47°48'W (135 m) (Kramp 1932a), two stations in Bredefjord, south Greenland (Kramp 1932b, 310–330 m and 700 m), Davis Strait (Levinson 1893, ca. 188–544 m; Kramp 1913, 700–1055 m; Broch 1918, ca. 544 m), western Greenland (Broch 1918, ca. 1095 m), Baffin Bay (Jäderholm 1909, ca. 731 m), 72°32'N–58°05'W (ca. 212 m), 60°27'N–48°31'W (Vervoort 1972, 326–366 m), 53°34'N–52°01'W (ca. 1792 m) and 52°25'N–52°12'W (ca. 296 m) (Jäderholm 1919), eastern Canada (Kindle & Whittaker 1917, ca. 365 m, based



on literature records), off northeast Newfoundland, 51°22'30"N–50°31'30"W (Calder 1970, 457 m, as *Cladocarpus cornutus*), Flemish Cap, Flemish Pass, and Grand Banks (present study), Northeast Channel, south of Nova Scotia, at 42°02'N–65°36'W (Henry 2001; personal communication, 24.11.2012), off Sable Island on Banquereau (Verrill 1879, ca. 365 m, first description; Nutting 1900; Whiteaves 1901; Fraser 1918, 1944), east of Gloucester (Massachusetts) (Fraser 1944, ca. 310 m). Not recorded further south by Henry *et al.* (2008), but there is a recent southern record from 53°56'S–63°51'W (250 m) by El Beshbeeshy (2011).

### ***Cladocarpus diana* Broch, 1918**

(Figs. 1B, 3A–G, tables 1, 4, 9, 11–12)

*Cladocarpus Diana* Broch, 1918: 87, fig. 47a–c.

*Cladocarpus diana*: Vervoort 1966: 149.—Schuchert 2001: 138, fig. 118A–D.—Bouillon *et al.* 2006: 283.

**Material examined.** FC07 L165, one fertile colony 7.0 cm high; FC07 L169, 3 fertile colonies, largest one 6.0 cm high; FC07 L171, one fertile colony 3.0 cm high; NEREIDA0509 RD15, 4 colonies, largest one 4.3 cm high, 3 fertile; NEREIDA0509 RD18, one fertile colony 4.7 cm high; NEREIDA0509 RD20, 5 colonies, largest one 5.8 cm high, 4 fertile; NEREIDA0609 RD36, one sterile fragment 1.5 cm high; NEREIDA0609 RD38, one sterile fragment 1.0 cm high; NEREIDA0610 RD62, 2 fertile colonies, largest one 2.7 cm high; NEREIDA0610 RD63, 2 fertile colonies, largest one 4.0 cm high, and a sterile fragment 1.4 cm high; NEREIDA0610 RD64, 3 colonies, largest 4.6 cm high, 2 fertile; NEREIDA0610 RD67, one fertile colony 5.0 cm high; NEREIDA0610 RD71, one sterile fragment 2.0 cm high.

**Description.** Colonies up to 7.0 cm high and 2.5 cm wide, formed by a root-like hydrorhiza consisting of a tuft of tubules supporting a polysiphonic stem, thinning out to monosiphonic distally. Stem light brown, flaccid when out of liquid, 0.9 mm wide proximally and tapering distally; distal part sometimes slightly geniculated. No ramification.

Main axial tube in front of stem and branches divided into 970–1200 µm long and 470–500 µm wide internodes by indistinct transverse nodes. Internodes with one apophysis more or less in middle, alternately right and left in successive internodes, giving rise to hydrocladia. Three nematothecae surrounding apophyses, one basal and two distal, one on each side. Accessory tubes scarce, parallel, with neither hydrothecae nor nematothecae.

Hydrocladia up to 1.65 cm long, alternate, spaced, given off at slightly acute angles with stem and branches, divided into up to 12 thecate internodes by more or less well-marked transverse nodes. Internodes with 6–7 internal septa (occasionally absent), one hydrotheca, and three one-chambered nematothecae. Hydrothecae large, deep, shorter than corresponding cormidia, with almost parallel walls in side view, but widening distally in frontal view; long axis parallel to that of internode, with depth/width at rim = 2.07–2.28 (n = 25). Perisarc thin, with a longitudinal mesial thickening on abcauline side. Intrathecal septum arising from behind hydrotheca, projecting forwards into its lumen, very reduced, thin, frequently oblique. Hydrothecal rim at right angle with the segment, with 9–11 cusps separated by deep embayments. Cusps rounded, sometimes uneven, with first abcauline pair clearly less pointed than others and almost blunt distally (Figure 3C).

Mesial nematothecae adnate to hydrotheca except on first internode, where there is a distinct gap between distal end of nematotheca and hydrothecal base. Aperture as wide as hydrotheca when seen frontally, rim smooth to sinuous, sometimes with an embayment in middle; distal end extending for 1/10–1/11 of adaxial hydrothecal wall. Lateral supra-calcine nematothecae arising oblique from hydrocladium, partially adpressed to distal hydrothecal wall, with aperture at level of hydrothecal rim; margin finely crenulated.

Phylactocarps up to 4.4 mm long, arising singly on hydrocladia, laterally from base of hydrotheca of first cormidium. They are formed by a first small internode devoid of nematothecae, followed by a jointed antler-shaped branched structure arching over the gonothecae. Branches normally three (occasionally up to four), each with a single row of nematothecae and some internal septa. Nematothecae with wide apertures and finely crenulated margins. Gonothecae 1–2 on each phylactocarp, attached by a small pedicel to points of ramification; obovate and curved distally, with lateral aperture tilted towards phylactocarp. Sex could not be ascertained.

**Remarks.** In material of the species described earlier, every phylactocarp divided dichotomously to form a structure of three branches (Broch 1918; Schuchert 2001). In some colonies examined here (NEREIDA0610 RD67), however, one of the branches may divide twice, resulting in a four-branch phylactocarp.

**TABLE 4.** *Cladocarpus diana* Broch, 1918. Measurements (in  $\mu\text{m}$ ) of colonies from different locations and sources. \*) Inferred from drawings.

	FC07 L165	NEREIDA0610 RD63	NEREIDA0610 RD67	Broch (1918)*	Schuchert (2001)
Colony					
Height (mm)	70	14–40	50	---	50
Hydrocladia					
Length of internode	1373–1600	1354–1430	1295–1460	1416	1314*
Diameter at node	165–217	125–163	167–190	125	200*
Hydrothecae					
Depth	1080–1194	1063–1106	1100–1134	983	1000
Diameter at rim	430–536	452–512	480–525	366	350
Nematothecae					
Length of laterals	226–242	201–217	190–206	150	200*
Diameter at level of terminal aperture	81–96	87–100	75–95	66	114*
Length of mesial	280–285	240–280	248–282	250	228*
Diameter of terminal aperture	----	----	----	250	257*
Gonothecae					
Length	1118–1165	----	1035–1043	833	1071*
Maximal diameter in frontal view	550–600	----	590–651	383	570*

The margin of the median inferior nematotheca is highly varied, although its position in relation to the hydrotheca is decidedly regular. Sometimes it is almost even, as depicted by Broch (1918), but at times it is deeply indented in the middle, roughly leaving two symmetric lobes and giving the impression of a bifid theca. Transitions between the two extremes occur. In most aglaopheniid species from the study area, the mesial nematotheca tapers distally when seen frontally, with its end rather thinner than its base. However, in *C. diana* the distal end is much wider than its base, being equal to the contiguous part of the hydrotheca.

The position of the centrally placed nematotheca on the internodes of the main tube varies. Normally, it is close to the apophysis, but sometimes the internodes are longer and the nematotheca is distant from it and is close to the proximal node instead (NEREIDA0610 RD63). One colony from this station is particularly delicate, having a thin stem and only a few accessory tubules, the hydrocladia are quite distant, and there are only a few phylactocarps. In addition, a colony from the Flemish Cap (FC07 L165), the largest known to date (7.0 cm high), has the longest internodes and deepest hydrothecae (Table 4).

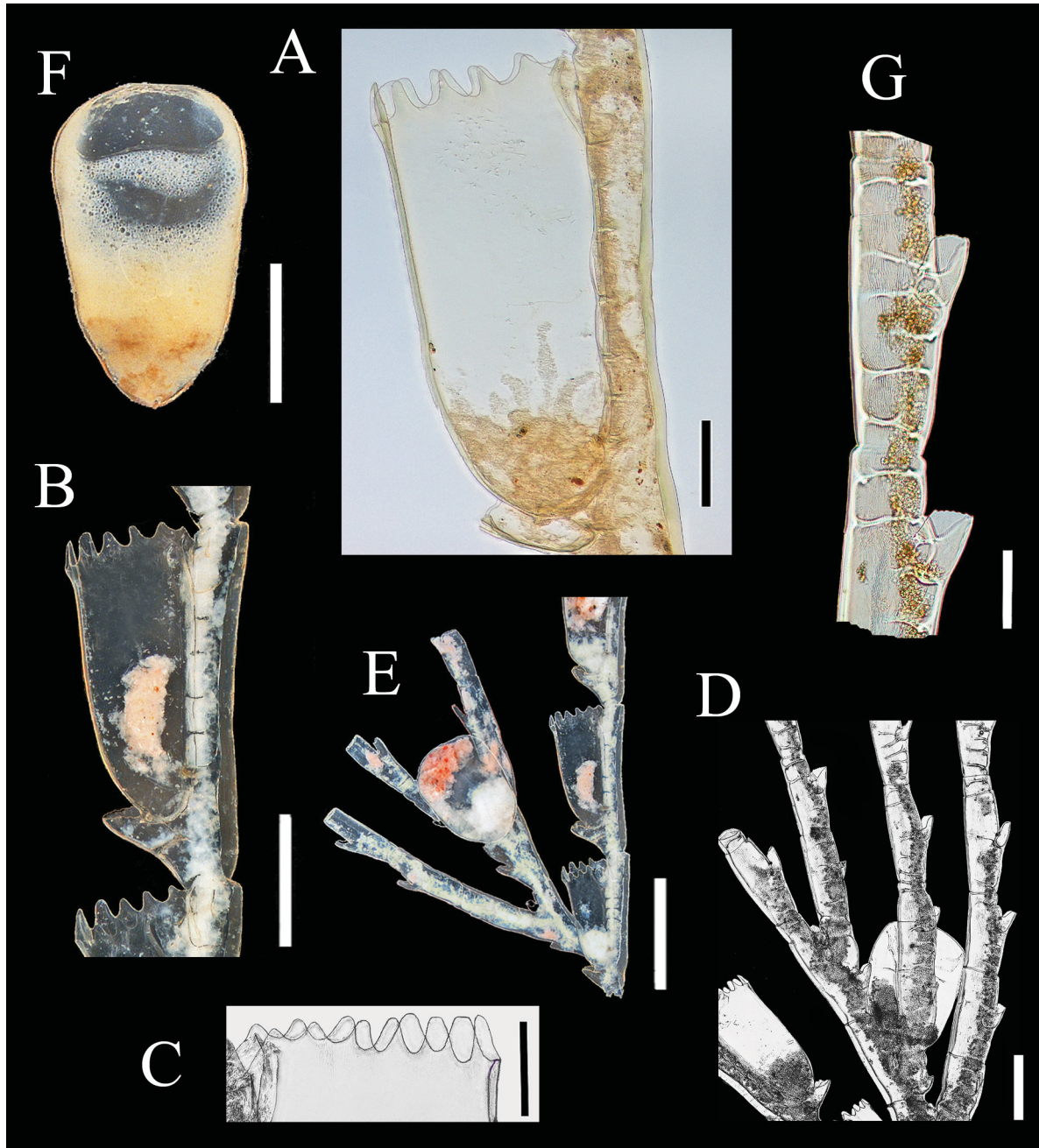
Broch (1918) observed hydrothecae on an outer branch of a phylactocarp, and regarded it as an abnormality. A similar observation was noted in one phylactocarp from NEREIDA0610 RD67.

Nomenclaturally, the specific name *diana* applied to this hydroid is taken to be a personal name formed as a noun in apposition. As such, the original spelling, *Cladocarpus diana* (first published as *Cladocarpus Diana*), is correct. While the Fourth Edition of the International Code of Zoological Nomenclature (ICZN) recommends avoidance of personal names as nouns in apposition (Recommendation 31A) to avoid possible confusion over authorship of the accompanying generic name, changing the species-group name *diana* to *dianae* in this case would result in an incorrect subsequent spelling (ICZN Art. 33.3).

**Observed depth range:** 600–1575 m. These are the shallowest and the deepest records, respectively, of the species, previously known only from European waters (south of Iceland) at depths of 1358–1504 m (Broch 1918).

**Fertile material.** Collected in July 2007 (838–1216 m depth), June and July 2009 (1071–1575 m depth), and June 2010 (600–1486 m depth).

**Distribution.** Previously known only from two stations south of Iceland (Broch 1918, ca. 1355–1504 m; Schuchert 2001). This is the first record of *Cladocarpus diana* in the western Atlantic, with collections from the Flemish Cap and the Beothuk Knoll. Present records also constitute the southernmost reports of the species.



**FIGURE 3.** *Cladocarpus diana* Broch, 1918. A, B) Hydrothecae. C) Detail of hydrothecal rim showing cusps; note that the first abcauline pair is almost blunt distally. D, E) Phylactocarps with gonothecae. F) Gonotheca in frontal view. G) Detail of a phylactocarp, showing internal septa. Scale bar: A, C, G= 200  $\mu$ m; B, D, F= 500  $\mu$ m; E= 1000  $\mu$ m. A, B, E, F= NEREIDA0610 RD63; C, D, E, G= NEREIDA0610 RD67.

### ***Cladocarpus formosus* Allman, 1874**

(Figs. 1C, 4A–H, tables 1, 5, 9, 11–12)

*Cladocarpus formosus* Allman, 1874: 478, pl. 68, fig. 1, 1a–b.—Kirchenpauer 1876: 26.—Allman 1877: 50.—Hartlaub 1896: 182.—Schneider 1898: 542.—Nutting 1900: 110.—Jäderholm 1909: 110.—Ritchie 1909: 310, fig. 1.—Billard 1910: 46.—Broch 1910: 207.—Kramp 1914: 1060.—Broch 1918: 85, fig. 45.—Jäderholm 1919: 11.—Bedot 1921: 325.—Kramp 1932a: 63.—Kramp 1932b: 20.—Kramp 1938: 39.—Kramp 1942: 21.—Kramp 1943: 44.—Vervoort 1966: 149.—Naumov 1969: 524, fig. 378.—Antsulevich 1987: 118.—Stepanjants 1989: 416.—Ramil & Vervoort 1992: 171.—Cornelius 1995: 205, fig. 48A–G.—Calder 1997b: 89.—Calder & Vervoort 1998: 54.—Ramil *et al.* 1998: 29.—Schuchert 2000: 413 (Table 1).—Desbruyères *et al.* 2001: 1334.—Schuchert 2001: 139, fig. 119A–D.—Moura *et al.* 2012: 720.



*Cladocarpus speciosus* Verrill, 1879: 311.—Nutting 1900: 116, pl. 28, fig. 8–11.—Whiteaves 1901: 28.—Kindle & Whittaker 1917: 233.—Fraser 1918: 361.—Fraser 1921: 179, fig. 106.—Fraser 1944: 41, pl. 90, fig. 399a–d.—Fraser 1946: 413.—Vervoort 1966: 149.—Calder 1997b: 89.

*Cladocarpus crenulatus* Levinsen, 1893: 210, pl. 8, fig. 13–14.—Vanhöffen 1897: 246.—Jäderholm 1909: 110.—Ritchie 1909: 314.

*Cladocarpus dubius* Broch, 1910: 207.—Kramp 1943: 44.

**Material examined.** FN3L06 L44, one fertile colony 9.0 cm high; FN3L06 L51, one fertile colony 7.0 cm high; FN3L06 L85, one fertile colony 9.5 cm high; PLA07 L70, 2 fertile colonies, largest one 8.0 cm high; PLA07 L86, one fertile colony 31.5 cm high; PLA07 L87, 2 colonies, largest one 22.0 cm high, one fertile; PLA07 L93, one fertile colony 19.1 cm high; PLA07 L101, one colony 19.5 cm high; FC07 L21, 2 colonies, largest one 12.1 cm high, one fertile; FC07 L23, one sterile colony 6.2 cm high; FC07 L155, one fertile colony 14.5 cm high; FC07 L166, 4 colonies, largest one 9.2 cm high, one fertile; FC07 L167, 2 fertile colonies, largest one 13.0 cm high; FC07 L171, one fertile colony 5.5 cm high; FN3L08 L66, one fertile colony 22.5 cm high; FN3L08 L88, 3 colonies, largest one 19.0 cm high, 2 fertile; FN3L09 L88, 3 colonies, largest one 44.0 cm high, one fertile; FN3L10 L35, one sterile colony 9.5 cm high; NEREIDA0509 RD4, 5 fertile colonies, largest one 8.3 cm high; NEREIDA0509 RD6, 5 colonies, largest one 10.1 cm high, 4 fertile; NEREIDA0509 RD10, 15 colonies, up to 11.0 cm high, some fertile; NEREIDA0509 RD12, 8 colonies, up to 11.5 cm high, some fertile; NEREIDA0509 RD15, 14 colonies, up to 11.7 cm high, some fertile; NEREIDA0509 RD18, 14 colonies, up to 10.8 cm high, some fertile; NEREIDA0509 RD19, 18 colonies, up to 12.8 cm high, some fertile; NEREIDA0509 RD20, 22 colonies, up to 12.7 cm high, some fertile; NEREIDA0509 RD21, 2 fertile colonies, largest one 8.5 cm high; NEREIDA0509 RD22, 20 colonies, up to 9.0 cm high, some fertile; NEREIDA0509 RD23, 21 colonies, up to 9.5 cm high, some fertile; NEREIDA0509 RD24, 34 colonies, up to 11.5 cm high, some fertile; NEREIDA0609 RD27, 5 colonies, largest one 11.0 cm high, some fertile; NEREIDA0609 RD28, 2 colonies, largest one 7.3 cm high, one fertile; NEREIDA0609 RD41, 6 colonies, up to 7.6 cm, some fertile; NEREIDA0709 RD49, 3 fertile colonies, largest one 8.8 cm high; NEREIDA0709 RD51, one fertile colony 14.3 cm high; NEREIDA0709 RD57, 2 fertile colonies, largest one 17.5 cm high; NEREIDA0709 RD59, 6 fertile colonies, largest one 14.2 cm high; NEREIDA0610 RD62, 20 colonies, up to 5.7 cm high, some fertile; NEREIDA0610 RD63, 12 colonies, up to 8.0 cm high, some fertile; NEREIDA0610 RD64, 9 colonies, up to 5.3 cm high, some fertile; NEREIDA0610 RD65, 51 colonies, up to 9.8 cm high, some fertile; NEREIDA0610 RD66, 50 colonies, up to 11.0 cm high, some fertile; NEREIDA0610 RD67, 5 fertile colonies, largest one 7.0 cm high; NEREIDA0610 RD71, 6 colonies, up to 6.0 cm high, some fertile; NEREIDA0610 RD74, 42 colonies, up to 17.0 cm high, some fertile; NEREIDA0710 RD76, 36 colonies, up to 13.5 cm high, some fertile; NEREIDA0710 RD77, 8 colonies, up to 12.5 cm high, some fertile; NEREIDA0710 RD78, one sterile fragment 2.7 cm high; NEREIDA0710 RD79, 2 fertile colonies, largest one 11.0 cm high; NEREIDA0710 RD80, 18 colonies, up to 14.2 cm high, some fertile; NEREIDA0710 RD83, 2 fertile colonies, largest one 6.0 cm high; NEREIDA0710 RD85, 9 colonies, up to 10.0 cm high, some fertile; NEREIDA0710 RD86, 9 colonies, up to 18.2 cm high, some fertile; NEREIDA0710 RD87, 26 colonies, up to 17.3 cm high; NEREIDA0710 RD88, 41 colonies, up to 17.5 cm high, some fertile; NEREIDA0710 RD92, 39 colonies, up to 20.5 cm high; NEREIDA0710 RD95, 13 colonies, up to 42.0 cm high, some fertile; NEREIDA0810 RD97, 16 colonies, up to 16.5 cm high, some fertile; NEREIDA0810 RD98, 7 colonies, up to 15.6 cm high, some fertile; NEREIDA0810 RD99, 14 colonies, up to 10.5 cm high, some fertile; NEREIDA0810 RD100, 30 colonies, up to 23.2 cm high, some fertile; NEREIDA0810 RD101, 10 colonies, up to 11.4 cm high, some fertile; NEREIDA0810 RD102, 2 colonies, largest one 8.8 cm high, one fertile; NEREIDA0810 RD103, 13 colonies, up to 27.5 cm high, some fertile; NEREIDA0810 RD104, 16 colonies, up to 53.5 cm high, some fertile.

**Description.** Colonies light brown to whitish in alcohol, plumose, occasionally ramified, up to 53.5 cm high, arising from root-like hydrorhizae consisting of tufts of tubules supporting the stems. Hydrorhiza sometimes also discoid (hard substrate). Stem erect, polysiphonic basally (3.0 mm wide), thinning out to monosiphonic distally. Branches long, arising at acute angles from stem, either irregularly or in subopposite pairs; sometimes second order branching present.

Main axial tube in front of stem and branches, divided into 850–1100 µm long internodes by more or less straight nodes. Accessory tubes parallel, not jointed, without hydrothecae, but with numerous nematothecae. Internodes with one apophysis close to distal end, directed alternately left and right, and with 3–4 nematothecae; 1–2 centrally placed and two axillar.

Hydrocladia up to 2.7 cm long, closely set, given off frontally at acute angles from apophyses of main tube. They are formed by up to 33 thecate internodes separated by transverse nodes, each with 8–10 internal septa



(generally 8). Internodes with one hydrotheca and three one-chambered nematothecae. Hydrothecae deep, not bulging into lumen of hydrocladium or only very slightly, almost totally adnate to internode, leaving only 1/10<sup>th</sup> free distally. Walls almost parallel, long hydrothecal axis forming an acute angle with the corresponding internode; depth/width at rim= 1.15–1.74 (n= 25). Intrathecal ridge of varied shape, length and development, thin and straight or sometimes almost circular, running from abcauline wall of hydrotheca towards internode, hardly reaching the latter. Margin wavy, with normally two outer cusps on abcauline side.

Nematothecae: one mesial proximal and two laterals. Mesial adnate to hydrotheca except on first internode, where there is a distinct gap between distal end of nematotheca and hydrothecal base, tapering distally, with slightly crenulated margin, extending for 1/2–4/5<sup>th</sup> the length of abaxial wall of hydrotheca; an oblique distal septum frequently present (Figure 4C, D). Lateral nematothecae mostly adnate to both internode and hydrotheca, tapering distally, tip slightly rising above hydrothecal margin; aperture adaxial, with finely crenulated margin.

Phylactocarps one per hydrocladium, 3.8 mm long, arising slightly laterally to first thecate internodes, between hydrothecal base and mesial nematotheca; antler-shaped, ramified, arching over the gonothecae, composed of a small internode followed by a dichotomously branched jointed structure. Branching normally of first order (though some additional branching may occur) and up to six branches. Nematothecae abundant, in a single adaxial row (occasionally abaxially), ending in a pair distally, all with margin finely crenulated. Gonothecae 1–2 on apophyses of main tube and up to 6 at forking of phylactocarps, obovate, distally truncated, curved, hooded, with lateral, narrowly oval aperture. Sex indeterminable.

**Remarks.** This species is morphologically varied, and our material comprises colonies with differences in structure of the thecate internodes that we attribute to intraspecific variability. There are two extreme morphs, although intermediate material is present as well. One of these extremes corresponds with material such as that described by Schuchert (2001). The other (Figure 4A) exhibits the following differences: i) the basal regions of hydrothecae bulge slightly into the lumen of the hydrocladium; ii) the terminal aperture of paired lateral nematothecae is slightly below the level of the hydrothecal margin; iii) the end of the mesial nematotheca extends for 3/5–4/5<sup>th</sup> the length of the abaxial hydrothecal wall; iv) the abaxial end of the hydrothecal ridge is curved backwards, so that it reaches back to the septum (hairpin shaped).

**TABLE 5.** *Cladocarpus formosus* Allman, 1874. Measurements (in µm) of colonies from different locations and sources.

	PLA07 L101	NEREIDA0610 RD74	FC07 L167	NEREIDA0610 RD74	Ritchie (1909)	Naumov (1969)
Colony						
Height (mm)	198	109	85–130	105	40–75	150
Hydrocladia						
Length of cormidium	739–782	648–681	730–775	822–957	840	580–790
Diameter at node	146–170	192–199	148–181	70–96	---	---
Hydrothecae						
Depth	523–685	435–596	600–700	518–563	570	440–580
Diameter at rim	349–399	376–424	338–405	340–398	350	310–350
Nematothecae						
Length of laterals	200–216	219–233	196–219	167–192	---	---
Diameter at level of terminal aperture	34–43	37–41	64–72	23–37	---	---
Mesial, diameter of terminal aperture	57–69	64–84	42–60	52–64	---	---
Mesial, distance from terminal aperture to hydrothecal margin	203–285	140–196	296–379	297–315	---	---
Mesial, length of free adcauline part	113–142	119–138	122–139	90–112	---	---
Gonothecae						
Length	---	1301–1390	1185–1210	---	1230	1000–1300
Maximal diameter in frontal view	---	674–725	650–700	---	700	500–700

One of the main differences between the two morphotypes is the shape of the intrathecal septum, which can be thin and straight (FC07 L167) or with its end arching backwards so that it sometimes reaches the septum again (NEREIDA0610 RD74, PLA07 L 101, Figure 4C). This character is highly variable. Levinsen (1893: pl. 8, fig. 13) depicted hydrothecae with a slightly curved adcauline end of the hydrothecal septum, and Naumov (1969: 526) discussed differences in structure of the intrathecal septum between *Cladocarpus speciosus* (now a synonym of *C. formosus*) and *C. formosus*, indicating that this character should not be considered of taxonomic importance in distinguishing between the two species. In the illustration of *C. speciosus* by Nutting (1900), the septum originates at the internode (see his pl. 28), while in the material studied here it begins at the abcauline wall of the hydrotheca and seldom reaches across to the internode.

The mesial nematothecae are adnate to the hydrothecae and their ends extend for 1/2–1/3 to 3/5–4/5 the length of the abaxial wall of the hydrotheca (Figure 4A, B). However, in the first cormidium, the mesial nematotheca is free from the hydrotheca (Figure 4F). This is related to the location of the phylactocarps, which occur on this internode and arise in the gap between mesial nematotheca and hydrotheca.

Internodes vary considerably in length, and so do the hydrothecae, as well as the proportion of the internodes occupied by the hydrothecae. In some colonies (FC07 L167), the hydrothecae extend along 75–86 % of the internode, whereas in others having smaller hydrothecae, only 60–68 % of the internode length is occupied (NEREIDA0610 RD74, see Table 5). The ratio hydrothecal length/width is also quite varied (between 1.15–1.74), with some hydrothecae almost as long as wide, while others are more than 1.5 times longer than wide.

Gonothecae occur on both the phylactocarp and apophyses (with 1–2 per apophysis) of the main tube (Figure 4F). Colonies with gonothecae, but lacking phylactocarps, were observed in material from several stations, including NEREIDA0610 RD74. Such specimens were usually small in size.

Cornelius (1995) noted that colonies of this species typically reach up to 8.0 cm, with specimens of as much as 15.0 cm reported by Naumov (1969). A specimen from station NEREIDA0810 RD104 was 53.5 cm high, a colony that must be considered exceptionally large.

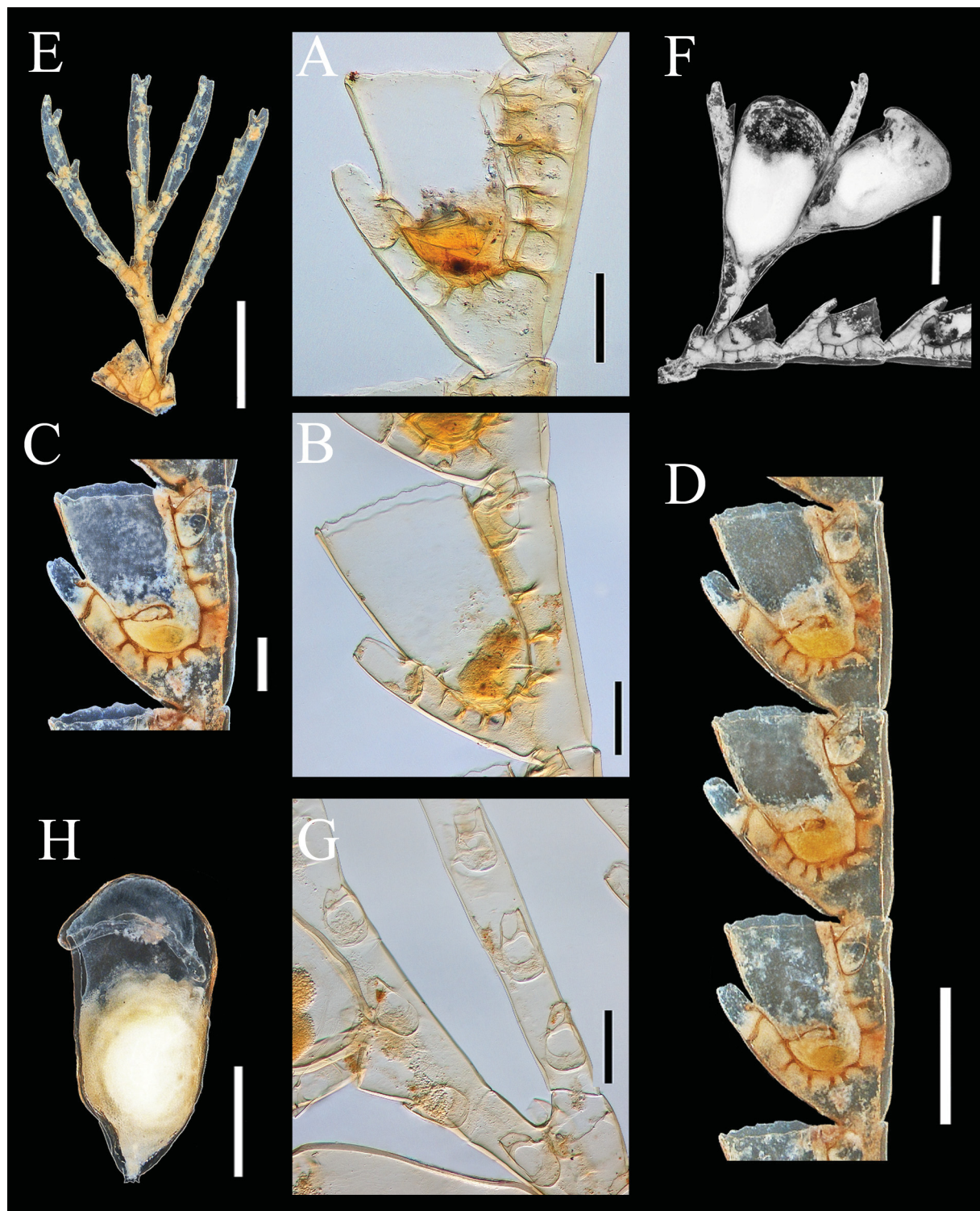
The development of the hydrothecal cusps varies, sometimes they being so little developed that the margin appears sinuous. Branching of the hydrocaulus is frequent at the distal end of the colony, and twin main stems arising from the same hydrorhiza sometimes occur. The shape of the phylactocarp and the position of gonothecae are identical in both types of colonies.

Fewkes (1881) provided a rudimentary account of an aglaopheniid he called *Aglaophenia crenata* from a fragmentary and unbranched colony dredged at 41°25'N–65°35'W (2270 m depth) off Massachusetts. Nutting (1900) redescribed and assigned it to *Cladocarpus*, despite the absence of a gonosome on the type, and he considered it very close to *C. speciosus*. His description agrees with the material of *C. formosus* studied here, colonies of which vary considerably in hydrothecal shape, intrathecal septum development, and position of the mesial nematotheca, and the two may be conspecific. That possibility is supported by the depth at which *C. crenatus* was collected, falling within the known depth range of *C. formosus*.

**Observed depth range:** 240–1885 m, within the range already known for the species. A neritic-bathyal species according to Calder (1997b), and also abyssal (*Cladocarpus speciosus*, 2602 m, continental slope east of Virginia, Fraser 1944; Calder 1997b).

**Fertile material.** Collected in August 2006 (240–1185 m depth), June and July 2007 (406–1381 m depth), August 2008 (1016–1198 m depth), from May to August 2009 (768–1885 m depth), and from June to August 2010 (520–1589 m depth).

**Distribution.** Kramp (1938) considered *C. formosus* to be a southern species in Iceland, perhaps following Broch (1910), who regarded it as a southern Atlantic hydroid recorded sporadically in the Arctic. According to Cornelius (1995), its distribution is circumpolar in sub-arctic to arctic waters.



**FIGURE 4.** *Cladocarpus formosus* Allman, 1874. A–C) Hydrothecae. D) Detail of a hydrocladium. E, F) Phylactocarps; note in F that, on the first cormidium, a distinct gap exists between the distal end of the mesial nematotheca and the hydrothecal base; compare it with the following internode of the hydrocladium. G) Detail of a phylactocarp showing nematothecae. H) Gonotheca in frontal view, showing hood. Scale bar: A, B, C, G= 200  $\mu$ m; D, F, H= 500  $\mu$ m; E= 1000  $\mu$ m. A= NEREIDA0610 RD74; B, F–H= NEREIDA0704 RD59; C–E= PLA07 L101.

*Cladocarpus formosus* is known from the Barents Sea, Sea of Okhotsk and the Kuriles (Naumov 1969, 80–1400 m; Antsulevich 1992, 42–60 m in an upwelling zone, and 130 + m out of this area), Faroe Channel (Ritchie 1909, 1030 m), Iceland (Broch 1918, ca. 83–847 m; Kramp 1938, 83 m; Schuchert 2001, 83–1020 m), Denmark Strait (Broch 1918, ca. 1444 m; Kramp 1938, 384–1444 m), Bredfjord in south Greenland (Kramp 1932b, 260–320



m), west coast of Greenland (Broch 1918, ca. 103–1096 m; Schuchert 2001, 187–200 m), Davis Strait (Levinsen 1893, ca. 150 m; Broch 1918, ca. 1041 m), 63°36'N–55°15'W, 60°16'N–47°48'W, 60°22'N–47°27'W (Kramp 1932a, 120–1200 m), 72°32'N–58°05'W, 69°16'N–58°08'W (Jäderholm 1919, ca. 212–335 m), eastern Canada (Kindle & Whittaker 1917, ca. 366 m, based on literature records), Flemish Cap, Flemish Pass and Grand Banks (present study), and Banquereau, off Sable Island (Verrill 1879, ca. 365 m; Nutting 1900; Whiteaves 1901; Fraser 1918, 1944). Not recorded further south in southeastern USA by Henry *et al.* (2008), but collected from Rainbow Vent Field, Mid-Atlantic Ridge (36°13'N, ca. 2400 m) (Desbruyères *et al.* 2001).

### ***Cladocarpus integer* (G.O. Sars, 1874)**

(Figs. 1D, 5A–F, tables 1, 6, 9, 11–12)

*Aglaophenia integra* G.O. Sars, 1874: 100, pl. 2, fig. 11–15.—Hincks 1874: 128.—Kirchenpauer 1876: 25.—Storm 1879: 24.—Storm 1880: 122.—Storm 1882: 23.—Marktanner-Turneretscher 1890: 277.—Bonnevie 1898: 14.—Bonnevie 1899: 93.—Nutting 1900: 117.—Bonnevie 1901: 13.

*Aglaophenia Moebii* Schulze, 1875: 134, pl. 2, figs. 3–5.—Kirchenpauer 1876: 25.

*Cladocarpus Pourtalesii* Verrill, 1879: 309.—Whiteaves 1901: 28.

*Cladocarpus Holmii* Levinsen, 1893: 209, pl. 8, fig. 15–18.—Saemundsson 1902: 70.

*Cladocarpus Holmi*: Vanhöffen 1897: 246.—Hartlaub 1900: 181.—Jäderholm 1909: 110.—Broch 1910: 207.—Kramp 1914: 1059.

? *Aglaophenia pourtalesii*: Bonnevie 1898: 13, pl. 1, fig. 11, 11a–b.—Bonnevie 1899: 93.

*Aglaophenia cladocarpa* G.O. Sars, in Bonnevie, 1898: 14 (nomen nudum).

*Cladocarpus pourtalesii*: Bonnevie 1898: 14.—Nutting 1900: 116, pl. 29, fig. 1–2.—Ritchie 1912: 230.—Kindle & Whittaker 1917: 233.—Cairns *et al.* 2002: 56.

*Cladocarpus pourtalesius*: Nutting 1900: 35.

*Cladocarpus holmii*: Hartlaub 1905: 675.—Linko 1912: 29, fig. 5.—Jäderholm 1919: 10.

*Halicornaria integra*: Jäderholm 1909: 109.—Ritchie 1912: 228, fig. 6.

*Cladocarpus pourtalesi*: Jäderholm 1909: 110.—Fraser 1918: 361.

*Aglaophenia moebiusi*: Bedot 1916: 44.—Stechow 1919: 135.

*Cladocarpus holmi*: Hartlaub & Scheuring 1916: 82.—Vervoort 1966: 149.—Naumov 1969: 523, pl. 19, fig. 5, fig. 376A–B.

*Aglaophenia moebieusi*: Bedot 1918: 61.

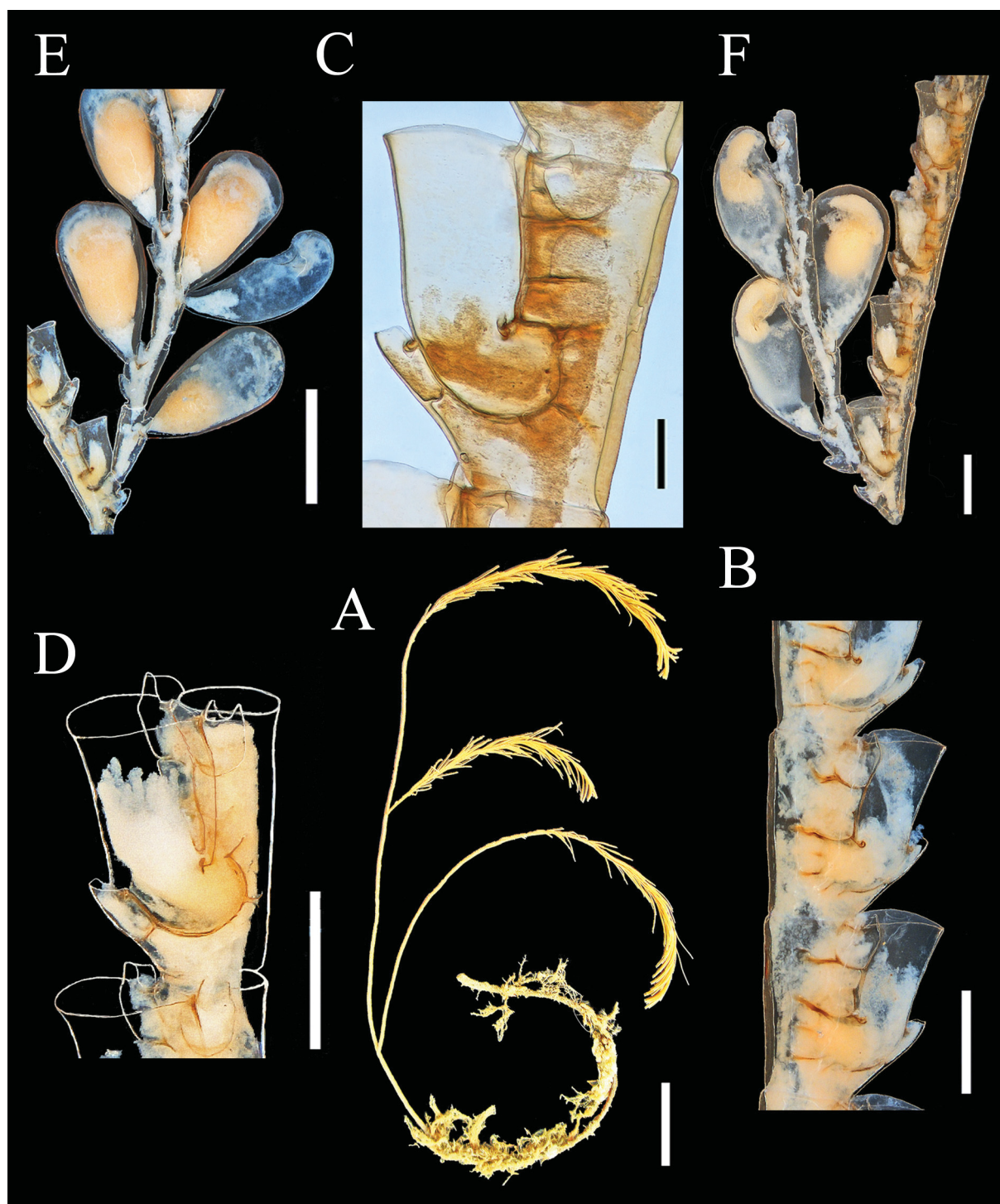
*Cladocarpus integer*: Jäderholm 1919: 10.—Kramp 1932a: 62.—Kramp 1935: 169, figs. 70, 71.—Kramp 1938: 39.—Kramp 1943: 44.—Vervoort 1966: 149.—Calder 1970: 1540, pl. 8.—Jägerskiöld 1971: 61.—Stepanjants 1989: 416.—Cornelius 1995: 208, fig. 49A–F.—Calder 1997b: 89.—Schuchert 2000: 413 (table 1).—Schuchert 2001: 140, fig. 120A–D.—Cairns *et al.* 2002: 22, 56.—Buhl-Mortensen & Mortensen 2005: 865.—Bouillon *et al.* 2006: 283.—Calder 2012: 63.—Moura *et al.* 2012: 721.

*Cladocarpus pourtalesi*: Fraser 1931: 7.—Fraser 1944: 407, pl. 89, fig. 395a–c.—Fraser 1946: 414.—Vervoort 1966: 149.—Bouillon *et al.* 2006: 283.

*Cladocarpus pourtelessii*: Stepanjants 1989: 416.

**Material examined.** FN3L06 L51, one fertile colony 56.0 cm high; FN3L06 L86, one fertile colony 62.0 cm high; PLA07 L61, one fertile colony 17.0 cm high; PLA07 L73, one sterile colony 13.2 cm high; PLA07 L75, one fertile colony 78.0 cm high; PLA07 L76, one sterile colony 45.0 cm high; PLA07 L77, one sterile colony 10.2 cm high; PLA07 L78, one fertile colony 10.0 cm high; PLA07 L80, one fertile colony 18.0 cm high; FC07 L23, one sterile colony 8.9 cm high; FC07 L123, one fertile colony 30.5 cm high; FN3L09 L80, one fertile colony 38.0 cm high; NEREIDA0509 RD7, one sterile colony 10.5 cm high; NEREIDA0509 RD9, one sterile colony 20.2 cm high; NEREIDA0610 RD62, one fertile fragment 1.7 cm high; NEREIDA0610 RD67, one fertile colony 8.0 cm high; NEREIDA0710 RD80, one sterile colony 4.7 cm high; NEREIDA0710 RD87, 2 sterile colonies, largest one 22.3 cm high; NEREIDA0710 RD88, 5 colonies, largest 41.8 cm high, 2 fertile; NEREIDA0710 RD89, 5 sterile colonies, largest one 25.3 cm high; NEREIDA0810 RD97, one sterile fragment 11.5 cm high; NEREIDA0810 RD98, one fertile colony 12.2 cm high; NEREIDA0810 RD99, 8 sterile colonies, up to 12.0 cm high; NEREIDA0810 RD100, one sterile colony 44.6 cm high.





**FIGURE 5.** *Cladocarpus integer* (G.O. Sars, 1874). A) Colony. B) Detail of a hydrocladium. C, D) Hydrothecae; D corresponds to the distalmost cormoid. Note distinctive bulging into lumen of hydrocladium. E, F) Phylactocarps with gonothecae; note on the first thecate internode that there is a distinct gap between distal end of nematotheca and hydrothecal base. Scale bar: A= 5.0 cm; B, D, F= 500  $\mu$ m; C= 200  $\mu$ m; E= 1000  $\mu$ m. A= PLA07 L75; B–F= PLA07 L61.

**Description.** Colonies large, plumose, ramified, up to 78.0 cm high, arising from a hydrorhiza consisting of a network of tubules, supporting the stems. Stem polysiphonic basally (up to 4.0 mm wide), thinning out to monosiphonic distally. Ramification in one plane, up to the second order. Branches arising at acute angles, up to 40.0 cm long in large colonies, polysiphonic for most of their length. Stem and branches brown to yellowish in alcohol.

Main tube in front of stem and branches, divided into 820–890  $\mu$ m long internodes by straight nodes.

Accessory tubes parallel, not jointed, without hydrothecae, but with numerous nematothecae. Internodes with one apophysis located almost in middle, directed alternately left and right, and two nematothecae: one frontal at base of apophysis, and another axillar.

Hydrocladia up to 3.5 cm long, abundant over entire colony, closely set, given off frontally at acute angles from apophyses of main tube, formed by up to 35 short internodes with 3–7 internal septa (normally 5–6) of varied length; perisarc thick. All internodes thecate, separated by more or less transverse nodes. Internodes with one hydrotheca and three nematothecae, all one-chambered and on frontal surface. Hydrothecae totally adnate to internode, inserting slightly obliquely, with walls almost parallel in side view and bulging deeply into lumen of hydrocladium. A small but stout intrathecal ridge arising from behind hydrotheca and pointing forwards. Margin even, with abaxial side slightly tilted downwards. Distal end of hydrothecae almost circular in cross section.

**TABLE 6.** *Cladocarpus integer* (G.O. Sars, 1874). Measurements (in  $\mu\text{m}$ ) of colonies from different locations and sources. \*) Including also data of Cornelius (1995). \*\*) As *Cladocarpus holmii*.

	PLA07 L61	Various authors*	Calder (1970)	Naumov (1969)**
Colony				
Height (mm)	165	Up to 230	65	210
Hydrocladia				
Length of internode	930–963	950–980	918–1090	720–800
Diameter at node	342–380	---	234–284	---
Hydrothecae				
Depth	716–852	430–800	635–735	670–730
Diameter at rim	404–460	290–420	334–418	350–400
Nematothecae				
Length of laterals	240–248	---	---	---
Diameter at level of terminal aperture	113–145	---	---	---
Length of mesial	270–284	---	---	---
Diameter of terminal aperture	74–79	---	---	---
Gonothecae				
Length	1330–1450	990–1100	---	1500
Maximal diameter in frontal view	635–715	350–400	---	700

Nematothecae: one mesial and two laterals. Mesial adnate to hydrotheca except on first internode, not tapering distally in front view, with even to slightly crenulated margin, two internal septa, extending 1/3–1.2/3 up abcauline wall of hydrotheca. Laterals mostly adnate to internode and hydrotheca, with distal end free; aperture adcaulinar, with margin finely crenulated to almost smooth.

Phylactocarps up to 5.5 mm long, arising slightly laterally on first cormidium, one per hydrocladium, between hydrotheca and mesial nematotheca. Not ramified, jointed, formed by a first small internode, and a series of up to 8 similar internodes, 550–700  $\mu\text{m}$  long and 180–250  $\mu\text{m}$  wide, separated by more or less transverse nodes, with a short apophysis and two nematothecae. Nematothecae consisting of one basal and two distal ones on either side of apophysis; margin finely crenulated. Each phylactocarp with up to 8 gonothecae; gonothecae obovate, curved towards phylactocarp with lateral aperture near distal end. Sex indeterminable.

**Remarks.** *Cladocarpus pourtalesii* Verrill, 1879 and *C. holmii* Levinsen, 1893 are generally considered synonyms of *C. integer* (Broch 1918; Schuchert 2001). Hydroids of all three nominal species have the basal regions of the hydrothecae bulging into the lumen of the hydrocladium (see Naumov 1969, fig. 376), and the shape of the thecate internodes is much alike (Figure 5C). Putative differences include the development and position of the mesial nematotheca on the thecate internodes, as well as the shape of the hydrothecae. Illustrations of *C. holmii*

from Davis Strait by Levinsen (1893), in his original description of the species, leave no doubt about its synonymy with *C. integer*. However, the basal regions of the hydrothecae of “*Aglaophenia pourtalesii*” from Norway, as illustrated by Bonnevie (1898), do not bulge into the internode, although the hydrothecal margin is clearly entire. If *C. holmii* and *C. pourtalesii* are indeed conspecific with *C. integer*, then the position of the mesial nematotheca is decidedly variable. According to Naumov (1969), it may be attached posterior to the base of the hydrotheca (as in *C. pourtalesii*), or it can be fused to the abcauline wall of the hydrotheca (as in *C. holmii*). No colonies belonging to the type of the former nominal species were seen during our study.

Due to the occasional absence of phylactocarps, or their development as simple, unbranched phylactogonia, *C. integer* has been considered a primitive species of the genus (Broch 1918). *Cladocarpus pourtalesii* has sometimes been distinguished from *C. integer* in having unbranched phylactocarps rather than unprotected gonangia (Nutting 1900). Otherwise, Nutting’s description of the species fully agrees with material of *C. integer* as first described by G.O. Sars (1874, pl. 2, fig. 12). Phylactocarps were present in all of the material we have seen, although we found some fertile colonies of *Aglaophenopsis cornuta* and *Cladocarpus formosus* lacking phylactocarps.

The size of the colony collected at station PLA07 L75, attaining 78.0 cm high, is considered exceptionally large. In previous reports, Nutting (1900) mentioned colonies of up to ca. 46.0 cm, Kramp (1932a) 23.0 cm high, and Schuchert (2001) 20.0 cm high.

*Cladocarpus integer* was recorded growing on *Primnoa resedaeformis* off Atlantic Canada by Buhl-Mortensen & Mortensen (2005), although no specific location was given.

**Observed depth range:** 119–1339 m. This is the deepest record of the species. A neritic-bathyal species according to Calder (1997b).

**Fertile material.** Collected in August 2006 (240–617 m depth), June and July 2007 (300–957 m depth), August 2009 (425–426 m depth), and from June to August 2010 (600–1100 m depth).

**Distribution.** Kramp (1938) considered *C. integer* as an Atlantic species, penetrating to some extent into arctic regions. It is known from the Barents Sea (Naumov 1969), Norway (Bonnevie 1898; Jäderholm 1909, ca. 183–365 m), Skagerrak (Kramp 1935, 80–90 m), Iceland (Broch 1918, ca. 254–260 m; Kramp 1938, 190–260 m; Schuchert 2001, 86–748 m), the east (Broch 1918, ca. 384 m) and west (Broch 1918, ca. 740–1096 m; Jäderholm 1919, 63°47’N–52°26’W, ca. 64 m; Kramp 1932a, 66°17’N–54°36’W, 97 m; Schuchert 2001, 191–195 m) coasts of Greenland, Davis Strait (Levinsen 1893, ca. 150–188 m; Broch 1918, ca. 150 m), Port Burwell (Ungava Bay) (Fraser 1931, 1944, no depth given), off northeast Newfoundland (Calder 1970, 457 m), eastern Canada (Kindle & Whittaker 1917, ca. 205–548 m, based on literature records), Atlantic Canada, no specific location (Buhl-Mortensen & Mortensen 2005, no depth given), Flemish Cap and Grand Banks (present study), three stations southeast of Cape Canso (Fraser 1944, ca. 164–243 m), Banquereau and southwest of Cape Sable (Nova Scotia) (Verrill 1879, ca. 205–548 m; Nutting 1900; Whiteaves 1901; Fraser 1918, 1944), and from off northern Florida to southwest of Cape Sable (Nutting 1900, ca. 164–548 m, *Albatross* stations 2474, 2479, 2666, 2698; Fraser 1944).

### *Nematocarpus ramuliferus* (Allman, 1874)

(Figs. 1E, 6A–J, tables 1, 7, 9, 11–12)

*Halicornaria ramulifera* Allman, 1874: 477, pl. 67, fig. 3, 3a–d.—Kirchenpauer 1876: 26.—Bale 1886: 90.—Schneider 1898: 538.—Nutting 1900: 126.—Broch 1903: 9.—Jäderholm 1909: 109.

*Halicornaria pluma* Broch, 1903: 8, pl. 4, fig. 15–21.

*Nematocarpus ramuliferus*: Broch 1918: 74, fig. 37a–d, fig. 38.—Kramp 1938: 38.—Kramp 1943: 44.—Ramil & Vervoort 1992: 175.

*Cladocarpus ramuliferus*: Schuchert 2000: 413 (table 1).—Schuchert 2001: 144, fig. 124A–F.—Bouillon *et al.* 2006: 283.

**Material examined.** NEREIDA0609 RD27, 3 fertile colonies, largest 2.6 cm high; NEREIDA0610 RD62, one sterile colony 1.5 cm high; NEREIDA0610 RD64, one fertile colony 3.0 cm high; NEREIDA0610 RD74, one sterile colony 3.8 cm high; NEREIDA0710, RD88, one fertile colony 4.2 cm high.

**Description.** Colonies light brown in alcohol, delicate, plumose, ramified, up to 4.2 cm high and 2.0 cm wide, arising from a poorly developed hydrorhiza consisting of a network of tubules that supports a polysiphonic stem basally, thinning out to monosiphonic distally. Stem flaccid, thin, erect, 0.4–0.5 mm wide proximally, tapering distally. Ramification in one plane, scarce. Branches up to 1.5 cm long, with thin axis (100  $\mu$ m), polysiphonic only basally, not opposite, arising at acute angles.

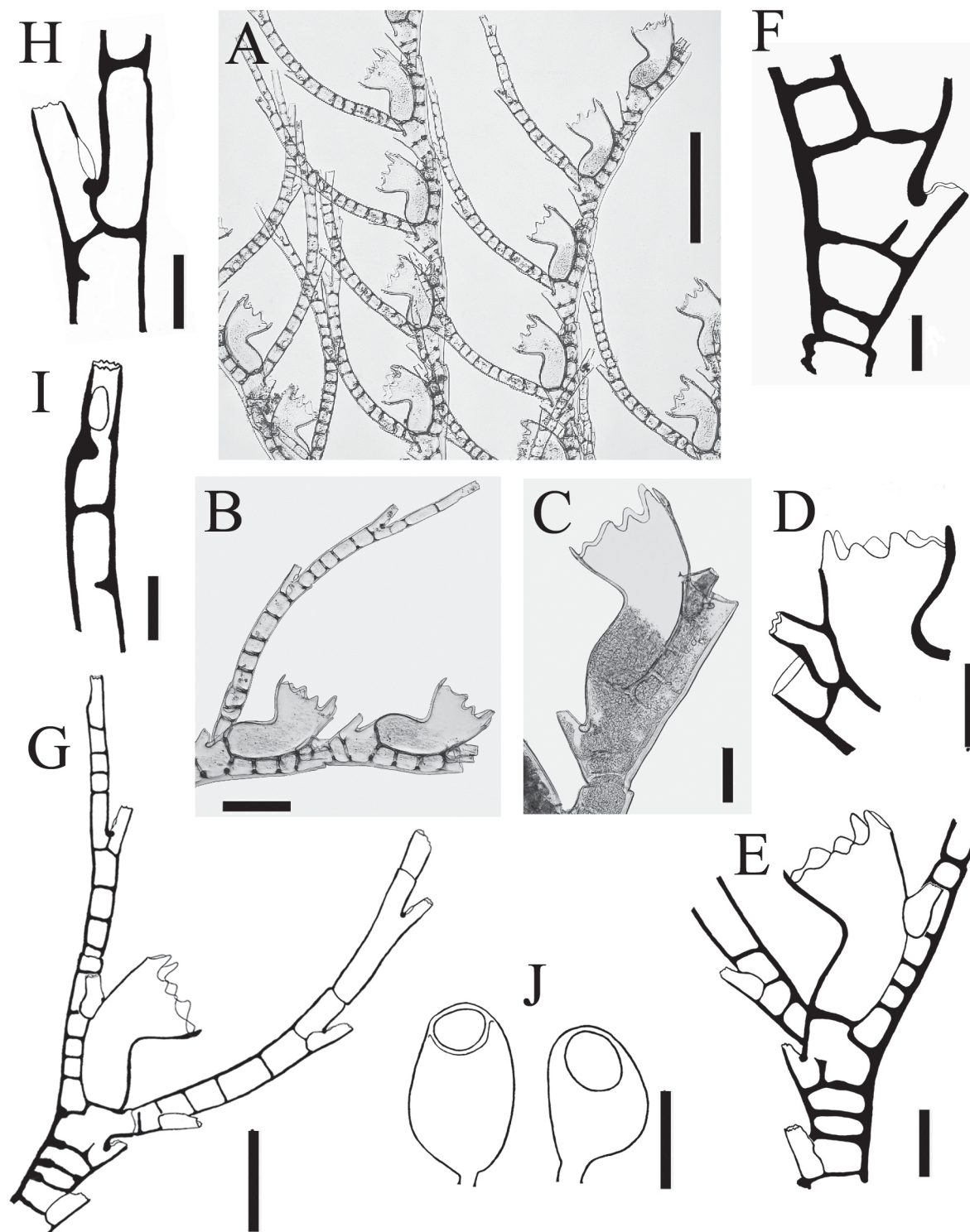
Main tube in front of stem and branches, divided into short (340–386  $\mu$ m) internodes by straight nodes. Accessory tubes parallel, not jointed, without hydrothecae and nematothecae. Internodes without internal septa, with one apophysis located in the lower half of internode, directed alternately left and right. Apophyses with two nematothecae: one frontal basally, the other distal, slightly above apophysis, somewhat lateral.

**TABLE 7.** *Nematocarpus ramuliferus* (Allman, 1874). Measurements (in  $\mu$ m) of colonies from different locations and sources. \*) Not precise, inferred from drawings.

	NEREIDA0610 RD64	NEREIDA0710 RD88	Broch (1918)*
Colony			
Height (mm)	30	42	---
Hydrocladia			
Length of internode	448–522	421–501	377–400
Diameter at node	52–81	56–68	78–89
Hydrothecae			
Depth	322–396	327–353	270–333
Diameter at rim	186–233	161–192	166–200
Nematothecae			
Length of laterals	91–102	98–103	90
Diameter at level of terminal aperture	21–35	21–27	42
Length of mesial	93–100	92–109	122–127
Diameter of terminal aperture	17–24	23–28	---
Length of those from ramuli	93–113	96–111	---
Diameter of terminal aperture	19–30	21–29	---
Gonothecae			
Length	---	328–477	425
Maximal diameter in frontal view	---	210–271	189

Hydrocladia abundant over entire colony, up to 6.0 mm long, given off at acute angles from apophyses of main tube, formed by up to 12 short internodes (Figure 6A). All internodes thecate, separated by more or less transverse nodes provided with 4–7 internal septa. Internodes with one hydrotheca and three one-chambered nematothecae. Hydrothecae widening distally, 45–65 % adnate to internode and 45–35 % free, strongly bent outwardly; perisarc thin, no intrathecal ridge. Margin with 7–11 pointed cusps, most commonly 10, not uniform in shape and size; typically with one mesial abaxillar, one mesial adcaulinar (sometimes doubled), and 4 symmetric pairs on both sides of hydrotheca; unpaired mesial abaxial cusp slightly tilted inwardly; first pair of adcaulinar ones longer than the others. Nematothecae include one mesial proximal, distant from hydrotheca, and two distal laterals (Figure 6C, F). Mesial with wide aperture and crenulated margin; laterals 58–51 % adnate to internode and hydrotheca and 42–49 % free, with aperture adcaulinar, slightly tapering distally; margin crenulated.





**FIGURE 6.** *Nematocarpus ramuliferus* (Allman, 1874). A) Hydrocladia; note abundance of ramuli and absence of gonothecae. B) Distal end of hydrocladium showing two thecate internodes and a ramulus. C, D) Distalmost hydrotheca of hydrocladium. E) Detail of a ramified ramulus with one hydrotheca; note abundance of internal septa. F) Mesial nematotheca from thecate internode. G) Ramified ramulus with one hydrotheca. H) Detail of a nematotheca from ramulus, showing proximal aperture. I) Distal end of ramulus showing terminal nematotheca with proximal, oval aperture. J) Gonothecae. Scale bar: A= 500  $\mu$ m; B, D, G, J= 200  $\mu$ m; C, E= 100  $\mu$ m; F, H, I= 50  $\mu$ m. A, F, J= NEREIDA0710 RD88; B–E, G–I= NEREIDA0610 RD64.

Most thecate internodes provided with long, segmented branches carrying nematothecae (ramuli), arising on abcauline side of hydrothecae between the insertion of mesial nematotheca and the hydrothecal base (Figure 6A, B, G). Ramuli 1587–1132  $\mu$ m long, 48–65  $\mu$ m wide proximally, and 28–30  $\mu$ m distally, arching over the hydrothecae,

gradually tapering distally; sometimes branched. Each ramulus jointed, with a short basal segment followed by 2–4 longer ones. Basal segment with no internal septa and no nematothecae, the others with 1–2 nematothecae aligned vertically on abcauline side and numerous septa, giving ramuli a chambered aspect. Distal end of ramulus with a nematotheca, with growing point slightly below (Figure 6I). Nematothecae of ramulus more or less tubular, slightly tapering distally, with two apertures: one rounded, terminal, with crenulated margin, and another one basal, ovoid, with smooth margin. Ramuli sometimes bearing a hydrotheca on one of their segments, hydrotheca similar to those from hydrocladia (only one hydrotheca per ramulus observed); if a hydrotheca is formed, a new ramulus arises from the space between the mesial nematotheca and the hydrothecal base.

Gonothecae ovoid, arising singly from the distal end of apophyses of main tube of stem and branches, one per internode. Pedicel short and thin, aperture almost round, wide, distal, lateral. Sex indeterminable.

**Remarks.** Broch (1903) described *Halicornaria pluma* as a new species, his hydroid closely resembling the present species, but having more ramified colonies and more numerous phylactocarps. These were present on all hydrocladia, and had a single hydrotheca. In our material, we observed both types of colonies, some having a few ramified ramuli with one hydrotheca, as described in *H. pluma*. The colony from Stn. NEREIDA0710 RD88 is the largest specimen of the species reported to date (4.2 cm in height).

As a rare and interesting species, *N. ramuliferus* has been mentioned infrequently in the literature. It is clearly distinct from other known aglaopheniids from the study area. Of the five species discussed here, it has the smallest hydrothecae. They are also distinctive in shape. Each is strongly bent forwards (up to 90°), with the aperture tilted abaxially and with a significant part of the adcauline side free. Its most striking feature, however, is the presence of segmented appendages with nematothecae (and sometimes also with a few hydrothecae) (Figure 6A, B, G). These appendages occur on all colonies collected, including those without gonothecae. Each of these ramuli is long and jointed, and given off somewhat laterally (as with phylactocarps of most *Cladocarpus* species) between hydrothecal base and mesial nematotheca from almost all the thecate internodes of the hydrocladia. The appendages are strongly septate and they arch over the hydrothecae. Their structure clearly resembles a phylactocarp, and they have been regarded as such by Schuchert (2001).

Confusion exists over the generic identity of this species because of the presence of hydrothecae on the ramuli. Moreover, uncertainty persists about the nature and function of the latter. It is unclear whether or not they are protective appendages for gonothecae. Originally assigned by Allman (1874) to the new genus *Halicornaria* (not *Halicornaria* Hincks, 1865), this hydroid has subsequently been referred to *Nematocarpus* (a monotypic genus containing *Halicornaria ramulifera*) by Broch (1918), to *Cladocarpus* by Schuchert (2001) and Bouillon *et al.* (2006), and tentatively to *Aglaophenopsis* by Bogle (1975) and Calder (1997a). *Halicornaria* Allman, 1874 is an invalid junior homonym of *Halicornaria* Hincks, 1865, while *Halicornaria* auct. is a junior synonym of *Gymnangium* Hincks, 1874, a genus in which gonangia lack protective organs and appendages with nematothecae. In *Nematocarpus*, the gonothecae occur on apophyses of the main tube and are said to be unprotected, although appendages with nematothecae, arising between the mesial nematotheca and the hydrothecal base, occur on almost all thecate internodes. In *Aglaophenopsis* and *Cladocarpus*, the gonothecae are borne on the stem, branches, and/or hydrocladia, and are protected by phylactocarps.

Inclusion of this species in *Halicornaria* and *Nematocarpus* shows that neither Allman (1874) nor Broch (1918), respectively, regarded the ramuli as protective organs for gonangia, a point of view held also by Leloup (1932). According to the latter author, ramuli were secondary hydrocladia having a different function from the phylactocarps of *Cladocarpus* and *Aglaophenopsis*. Moreover, the diagnosis of *Nematocarpus* by Broch (1918) clearly states that “gonangia are not surrounded by any protective organs”. In describing *Halicornaria pluma* (= *H. ramulifera*) earlier, Broch (1903) noted that a new genus should be erected for this peculiar species, and he did so later on (Broch 1918, as *Nematocarpus*).

Other authors, however, have considered the ramuli as protective organs and have rejected *Aglaophenopsis*, *Nematocarpus*, or both, and merged them into *Cladocarpus* (Stechow 1913: 26; Bedot 1921; Bogle 1975; Millard 1975; Bouillon 1985; Schuchert 2001; Bouillon *et al.* 2006). Their function remains obscure. Vervoort (1966) stated that even in the presence of phylactocarps, the limitations of *Cladocarpus* from *Aglaophenopsis* and *Nematocarpus* are far from clear. Calder (1997a) and Ramil & Vervoort (2004) for instance, regarded *Nematocarpus* as congeneric with *Aglaophenopsis* and distinct from *Cladocarpus*. Their opinion was based on the supposition that ramuli were phylactocarps occurring on several internodes.

In our opinion, ramuli of this species are not solely protective organs for the gonothecae. They function

instead, in part or in whole, as a protection for the hydranths. Moreover, the structure of phylactocarps of *Cladocarpus* differs from those of *Aglaophenopsis* (see Bogle 1975) and from ramuli of *Nematocarpus*. Thus, in our opinion Allman's *Halicornaria ramulifera* belongs to a genus other than *Cladocarpus*, either *Aglaophenopsis* or *Nematocarpus* (Table 8). We offer five reasons to support our conclusion: i) all the colonies examined had many ramuli, but not all bore gonothecae (Figure 6A), the presence of the former not being necessarily related to the presence of the latter; ii) ramuli occur on almost all of the thecate internodes of the colony, rather than only the proximalmost ones, as in *Aglaophenopsis* and *Cladocarpus* (with one phylactocarp per hydrocladium); iii) the gonothecae are borne on the apophyses of the main tube that support hydrocladia, and not on the ramuli; iv) the ramuli are always curved over the hydrothecae (with the nematothecae occurring in a row on the outer, convex side) and not over the gonothecae (Figure 6B); v) the ramuli are strongly septate, with a chambered structure. As for point ii), see discussion below on *Cladocarpella multiseptata* Bale, 1915.

**TABLE 8.** Main distinguishing characters of the genera *Aglaophenopsis*, *Cladocarpus*, and *Nematocarpus*.

	Gonothecae	Phylactocarps/ramuli
<i>Aglaophenopsis</i>	On apophyses of main tube and/or on phylactocarp	Borne only on proximalmost cormidia; they are either a modified mesial nematophore (or a modification of one of the funnels when the nematotheca is bifid), or arise laterally from the hydrothecal base; hydrothecae always present. Internodes of phylactocarp strongly septate. Protection of gonothecae.
<i>Cladocarpus</i>	On apophyses of main tube and/or on phylactocarp	Borne only on proximalmost cormidia, between the mesial nematotheca and the hydrothecal base. Protection of gonothecae.
<i>Nematocarpus</i>	On apophyses of main tube, never directly on the ramuli	Borne on almost all thecate internodes of hydrocladia, between mesial nematotheca and hydrothecal base; they can develop into secondary hydrocladia; hydrothecae sometimes present. Internodes of ramuli strongly septate, giving them a chambered structure. Doubtfully protecting gonothecae; certainly protecting the hydranths.

In *Aglaophenopsis*, protective structures (phylactocarps) occur only on the proximalmost internodes of hydrocladia, are strongly septate, and bear hydrothecae (Figure 2C). In the type species, *Aglaophenopsis hirsuta* Fewkes, 1881 (but not in all species currently assigned to the genus), they are a modification of the mesial nematophore, replacing it (Fewkes 1881; Bale 1886) (Table 8). In *Cladocarpus*, the phylactocarp is not so strongly septate, lacks hydrothecae, and does not replace the mesial nematophore; instead, it is an appendage originating generally in the space between the mesial nematotheca and the hydrothecal base. In both genera, gonothecae arise both from apophyses of the main tube and from the phylactocarps.

In *Nematocarpus*, protective structures are strongly septate and may have hydrothecae on the ramuli, as in *Aglaophenopsis*. However, these structures commonly occur on all of the thecate internodes (only the basalmost of which afford significant protection to gonothecae), are borne between the mesial nematotheca and the hydrotheca (i.e., they do not replace the mesial nematotheca), and the gonothecae never arise from the ramuli. For these reasons, we recognize *Nematocarpus* as a valid monotypic genus, distinct from *Aglaophenopsis* and *Cladocarpus*, with *N. ramuliferus* as its only known species.

Appendages similar to these ramuli occur in the genus *Calvinia* Nutting, 1900. A genus included in Halopterididae Millard, 1962 by Bouillon *et al.* (2006), it is poorly known and not possible, at present, to determine its systematic position (see Peña Cantero *et al.* 2010). These appendages were considered as protective structures for the hydrothecae (hydranths) by Nutting (1900) and Fraser (1944), and are present on all of the thecate internodes of a cladium. The gonothecae are borne only on the first internode of the hydrocladia, “springing from the side of the proximal nematophorous branch” (Nutting 1900). According to Nutting, his newly described species—*Calvinia mirabilis* Nutting, 1900—was the only “Eleutheroplean” that “has produced a nematophorous branch for the protection of each hydrotheca”. In both *C. mirabilis* and *Nematocarpus ramuliferus*, these protective structures occur on most, if not all, thecate internodes of the hydrocladia. The genus *Calvinia* was accepted as valid by Bouillon *et al.* (2006) based on the development of these structures, and they were used as a discriminatory character in their identification key to genera of Halopterididae. Recognition of *Nematocarpus* as a distinct genus appears warranted on the same grounds.



*Cladocarpella* Bale, 1915, synonymized with *Cladocarpus* by Billard (1918), likewise has appendages with nematothecae on more than one internode per hydrocladium. According to Billard, the genus fully agrees with the diagnosis of *Cladocarpus* by Allman (1874) in that protective branches are appendages from the hydrocladia. However, *Cladocarpella multiseptata* was moved into *Streptocaulus* Allman, 1883 by Ramil & Vervoort (2008) due to the structure of the phylactocarps. Fertile colonies of *Streptocaulus multiseptatus* from the Bay of Biscay (Avilés Canyon System, north of Spain, INDEMARES 2010 project, stn. RD01, 06°06.8150'W–43°52.000'W, 266 m depth, unpublished data), have phylactocarps on 2–3 thecate internodes of the same hydrocladium, that arise between the mesial nematotheca and the hydrothecal base, and not only on the proximal thecate internode. Unlike *Nematocarpus ramuliferus* and *Calvinia mirabilis*, all phylactocarps have gonothecae, and nematothecae are paired and opposite.

**Observed depth range:** 605–1091 m, according to data from the literature.

**Fertile material.** Collected in June 2009 (846–859 m depth), and June–July 2010 (676–1091 m depth).

**Distribution.** Thought to be a visitor to northern European waters from warmer and deeper parts of the Atlantic Ocean (Broch 1918; Kramp 1938). It is a rare species, known previously only from a few stations in the northeastern North Atlantic. Records exist from east and west of the Faroes and Shetland Islands (Broch 1903, 1026 m), Iceland (Broch 1918, ca. 260 m; Kramp 1938, 260 m; Schuchert 2001, 196–1508 m), and now the Flemish Cap and slope of the Grand Banks (present study). Present records constitute the first report of the species in the western Atlantic, and they extend its known latitudinal range further to the south.

## Discussion

The discovery of five aglaopheniid species off the east coast of Newfoundland, two of them not recorded previously in the western North Atlantic, is noteworthy. Aglaopheniids are predominantly a warm-water group of hydroids (Calder 1997a), and their diversity is low in cold Atlantic waters (Fraser 1944). Only eight species are known previously in the region from 40°N (New York Bight) northwards to the Arctic Ocean in northeastern North America (Table 1), and most of those have been reported infrequently. However, biodiversity of the deep-water fauna in this region is comparatively less well known than at equivalent latitudes in the northeast Atlantic. For example, 12 species of aglaopheniids (11 of *Cladocarpus* Allman, 1874 and one of *Lytocarpia* Kirchenpauer, 1872), were reported by Schuchert (2001) from waters around Iceland, and a greater number are known from 40°N northwards in European waters (Cornelius 1995; Altuna 2007). Based on current knowledge, species richness in the family therefore appears to be higher at a given latitude in the northeastern than in the northwestern Atlantic. The disparity in species richness, particularly at shallow depths, may be due in part to differences in sea temperatures at a given latitude in North America and Europe. However, there has also been unequal sampling effort and taxonomic work in the two regions. For instance, Kramp (1943, table 2), listed six species from the west coast of Greenland, while only three were known previously from eastern Canada.

*Aglaophenopsis cornuta*, *Cladocarpus formosus*, and *Cladocarpus integer* are quite widely distributed (although infrequently reported) from the Davis Strait and Baffin Bay regions southwards at least to Newfoundland. In contrast, *Cladocarpus diana* and *Nematocarpus ramuliferus* are new records for the northwestern North Atlantic. Both occur on the Flemish Cap, a location where all species dealt with in this paper were recorded (Table 11). The Flemish Cap is a plateau of approximately 200 km width, with depths of less than 150 m at its center. Situated eastward of the Grand Banks of Newfoundland, it is separated from those banks by the approximately 1200 m deep Flemish Pass (Figure 1). The Flemish Cap is located within an area of transition between cold subpolar waters and is influenced by fluctuations in the Labrador Current and in the North Atlantic Current (Gil *et al.* 2004). Compared with the Grand Banks, the Flemish Cap supports higher primary and secondary productivity due to its hydrodynamic conditions (Maillet *et al.* 2005). The mix of different currents in the area (Gil *et al.* 2004), a highly oxygenated environment rich in nutrients (Stein 2007), and greater substratum heterogeneity on the Flemish Cap compared with adjacent areas may explain differences in its faunal composition. It is a poorly studied area, and one in which rare and seldom-recorded species of other animal groups, such as deep-sea corals (Murillo *et al.* 2011), are not uncommon. According to those authors, species exist on the Flemish Cap

**TABLE 9.** Some morphological characteristics of the species discussed herein.

	<i>A. cornuta</i>	<i>C. diana</i>	<i>C. formosus</i>	<i>C. integer</i>	<i>N. ramuliferus</i>
Depth of hydrothecae ( $\mu\text{m}$ )	703–794	1063–1194	435–700	716–852	322–396
Abcauline keel on abcauline side of hydrothecae	Yes, extending beyond level of hydrothecal margin	No, but there is a thickening of the perisarc	No	No	No
Intrathecal septum	Small, arising from rear wall and directed frontally	Small, arising from back wall and directed frontally	Variable; straight and thin, or long, curved, bent distally in middle	Small, arising from back wall and directed frontally	Absent
Rim of hydrothecae	Cusped, 9–11 cusps	Cusped, 9–11 cusps	Wavy, 2 abcauline mesial cusps	Even	Cusped, 7–11 cusps
Basal region of hydrothecae bulging into lumen of hydrocladium	No	No	No, sometimes slightly	Yes, prominently	No
Internal septa of thecate internodes	2–9	6–7	8–10	3–7	4–7
End of mesial nematothecae in thecate internodes	1/3–1/2 up hydrotheca	1/10–1/11 up hydrotheca	1/2–4/5 up hydrotheca	1/3–1.2/3 up hydrotheca	Not reaching hydrotheca
Hydrothecal aperture	At right angle to hydrocladial axis	At right angle to hydrocladial axis	At right angle to hydrocladial axis	At right angle to hydrocladial axis	Strongly tilted abaxially
Ramuli	No	No	No	No	Yes
Gonothecae	On phylactocarp	On phylactocarp	On phylactocarp and apophyses of main tube	On phylactocarp or stem (apophyses ?) according to Broch (1918)	On apophyses of main tube
Nematothecae on the accessory tubes of stem	No	No	Yes	Yes	No
Hydrothecae on phylactocarps or ramuli	Yes	No	No	No	Yes
Maximal size of colony (cm)	28.7	7.0	53.5	78.0	4.2

**TABLE 10.** Some characteristics of species assigned to *Aglaophenopsis* Fewkes, 1881. \*) Margin is at times deeply indented in the middle, giving the impression of a twin theca.

	<i>A. bonnevieae</i> (Jäderholm, 1909)	<i>A. cartieri</i> (Bedot, 1921)	<i>A. cornuta</i> (Verrill, 1879)	<i>A. (?) distans</i> Nutting, 1900	<i>A. hirsuta</i> Fewkes, 1881	<i>A. vaga</i> Briggs, 1918	<i>A. verrilli</i> Nutting, 1900
Phylactocarp (arising from proximal segment of hydrocladia)	Alternately branched, precise origin not clear from literature	Unbranched, originating laterally between mesial nematotheca and hydrothecal base	Forked (Y-shaped), originating laterally between mesial nematotheca and hydrothecal base	Unbranched, origin not clear from literature	Occasionally branched, arising from one of the funnels of the mesial nematotheca	Unbranched, originating laterally between mesial nematotheca and hydrothecal base	Forked (Y-shaped), originating laterally between mesial nematotheca and hydrothecal base
Substitution of mesial nematotheca by the phylactocarp	No (?)	No	No	Unclear	Yes, of one of the funnels	No	No
Hydrothecae on phylactocarp	Yes, numerous	Unclear, possibly occurring	One terminal on each of the two branches	Yes	Yes, toward distal end	1–2 terminal	Yes. One terminal on one of the branches and a row on the other
Gonothecae	Ovoid to pear-shaped	Ovoid	Obovate	Sub-cylindrical	Ovoid	Oblong-ovate	Obovate
Aperture of gonothecae	Oval, subterminal	Circular, terminal	Broadly oval to almost circular, latero-terminal	Unclear information available	Circular, terminal	Pear-shaped, latero-terminal	Unclear information available
Mesial nematotheca	single	single	single*	single	bifurcated	single	single
Remarks	--	--	--	Probably not valid. Not recorded since original description	Type species of the genus	--	--
Distribution	North Atlantic	Azores, Mid-Atlantic Ridge	North Atlantic	Off southern Florida	Sub-tropical western Atlantic	New South Wales	Northern Virginia to Georges Bank



that are not usually recorded in deep-waters off the Canadian coast, and species richness is higher compared with more extensive areas immediately to the west. Such faunal differences probably also exist in the hydroid fauna, but no investigations have been undertaken to support this assumption.

As noted in the Introduction, genera of Aglaopheniidae are differentiated mainly on the basis of gonosomal characters. Of eight genera recognized in the family worldwide by Bouillon *et al.* (2006), *Cladocarpus* is second in terms of diversity, with 66 species of mostly deep-water forms. Two approaches have been adopted in the taxonomy of this group of aglaopheniids. One of these, adopted by Bouillon *et al.* (2006) and others, is to recognize a broadly defined genus *Cladocarpus*, treating it essentially as a collective group until questions of relationships become clearer. The second approach is to refer *Cladocarpus*-like hydroids to several genera, distinguishing them largely by differences in morphology of their phylactocarps that are thought to reflect relationships. Following this approach, Ramil & Vervoort (1992) distinguished between species having a phylactocarp homologous to the axis (*Cladocarpus* s.l.) from those in which the rachis is similar structurally to the hydrocladia (*Streptocaulus*). Their proposals have not been widely accepted because of the existence of intermediate material with respect to this character (see Schuchert 2001). Given the present limited knowledge, actual relationships thus remain obscure. Phylogeny of the group should become clearer as cladistic studies and molecular analyses are undertaken. Particular attention in such investigations must be given to the type species of the various putative genera. Whichever taxonomic approach is followed now, revisions in classification and nomenclature can be expected, although we maintain that fewer changes will be likely to take place when the second alternative is adopted. We therefore support recognizing various genera within this group based on available evidence, rather than simply assigning a large and diverse assemblage of species to an excessively broad *Cladocarpus*. The genus is already species-rich, and adding many dissimilar taxa to it overextends its scope and renders it more difficult to conceptualize and refine. In our opinion, several nominal genera included in the synonymy of *Cladocarpus* sensu lato will almost certainly be recovered as valid based on differences in structure of the phylactocarp. In any case, reproductive structures in species of *Cladocarpus*, as conceived by Bouillon *et al.* (2006), are heterogeneous. All five species recorded herein were assigned to the same genus (*Cladocarpus*) in that work, notwithstanding significant variation in morphology of their gonosomes (and in one case colony structure). We conclude that the five species are referable to three genera, viz. *Cladocarpus*, *Aglaophenopsis*, and *Nematocarpus*.

**TABLE 11.** List of species, depth interval (m), depth range (m), and number of stations at which each species was collected in the three sampling areas. FC, Flemish Cap; FP, Flemish Pass; GB, Grand Banks. Depth range is the difference in meters between the shallowest and deepest records. The coldest bottom temperature (−0.42°C), recorded with a collection of *Cladocarpus integer*, was from the shallowest collection site (on the Grand Banks).

Species	FC	FP	GB	Depth interval	Depth range	Bottom temperature °C	Gonosome
<i>Aglaophenopsis cornuta</i>	14	19	18	240–1885	1645	2.68–4.42	May to August
<i>Cladocarpus diana</i>	13	--	--	600–1575	975	3.40–3.95	June, July
<i>Cladocarpus formosus</i>	26	15	24	240–1885	1645	2.68–4.12	May to August
<i>Cladocarpus integer</i>	6	3	15	119–1339	1220	−0.42–4.11	June to August
<i>Nematocarpus ramuliferus</i>	2	2	1	605–1091	486	3.50–4.01	June, July

The taxonomy of *Cladocarpus formosus* is unmistakable, as it is the type species of the genus. *Cladocarpus diana* is also referable to *Cladocarpus* based on characters of its reproductive structures. The generic identity of *Cladocarpus integer* is less clear. Its phylactocarp is an unbranched structure and as such is dissimilar to that of *C. formosus*. Still, species with both branched and unbranched phylactocarps are currently assigned to *Cladocarpus*, and we include *C. integer* in that genus for the time being.

The status of *Nematocarpus*, and the generic affinities of its sole species *N. ramuliferus*, are unclear. *Nematocarpus* is closely related to *Aglaophenopsis*, and the two were regarded as congeneric by Calder (1997a). Hydrothecae and ramuli/phylactocarps of *Aglaophenopsis hirsuta* Fewkes, 1881 (type species of *Aglaophenopsis*) and *Nematocarpus ramuliferus* (Allman, 1874) (type species of *Nematocarpus*) are quite similar, as apparent in illustrations of *A. hirsuta* by Vervoort (1972: 206) and *N. ramuliferus* by Broch (1918: 76) and Schuchert (2001: 144). Gonothecae and overall colony forms of the two are also similar. However, ramuli of *N. ramuliferus* are not

restricted to the proximalmost cormidia, as occurs with the phylactocarps of *Aglaophenopsis* and *Cladocarpus*, and the gonothecae are borne only on the apophyses of the main tube of stem and branches, and not on the ramuli. Hence, ramuli do not appear to function primarily as reproductive structures protecting the gonothecae, as is the case with phylactocarps of *A. hirsuta*. Hydroids belonging to the genus *Calvinia* (Halopterididae) are recognized as distinct based on possession of such accessory tubules, and the same character provides justification for recognition of *Nematocarpus*. Thus, *Nematocarpus* is upheld here as a valid genus, containing its type species, *N. ramuliferus*.

Some seven species have been assigned to *Aglaophenopsis*, with six of them occurring in the North Atlantic (Table 10). The phylactocarp in the type species, *A. hirsuta* Fewkes, 1881, arises in place of the mesial nematotheca (Fewkes 1881). Vervoort (1972) noted that it was borne on one of the funnels when the nematotheca is bifid. This difference was clearly stated by Bale (1886), who noted that “the phylactocarps of *Aglaophenopsis* are modified from the mesial nematophore of the proximal hydrothecae, while in *Cladocarpus* they are independent structures, and the genus must rest on this distinction”. The emended diagnosis of the genus by Fraser (1944) asserts that the gonosome is “protected by phylactogonia that appear to be modified mesial nematophores”. However, Bogle (1975) did not mention phylactocarps as modified mesial nematothecae in her diagnosis of the genus, stating: “phylactogonia arising singly from the proximal internode of unmodified hydrocladia from an area to the side and slightly above the mesial nematotheca”. In fact, not all species referred to *Aglaophenopsis* have modified mesial nematothecae (see Table 10). Bogle emphasized the presence of hydrothecae on the phylactocarps as a distinction from *Cladocarpus* in her key to genera, and proposed other characters for differentiation. Accordingly, we are uncertain about the correct generic assignment of *Cladocarpus cornutus* Verrill, 1879 (and *Aglaophenopsis bonnevieae*, which we regard as congeneric with *A. cornuta*). While both species are usually referred to *Aglaophenopsis*, we question whether they are congeneric with *A. hirsuta*, type species of that genus, because their phylactocarps are different. In both *A. cornuta* and *A. bonnevieae* they are forked (‘Y-shaped’, or even alternately branched in large colonies of *A. bonnevieae*) and consistently hydrothecate, usually throughout (e.g., see Kramp 1932a: 59; Schuchert 2001: 138) (Figure 2C). Instead, those of *A. hirsuta* (see Nutting 1900: pl. 29, fig. 12; Vervoort 1972: 206) are unbranched, and hydrothecae are of sporadic occurrence. Gonothecae also seem to differ, especially those of *A. cornuta*, apertures of which are lateral and oval in shape, rather than terminal and circular as in *A. hirsuta*. These two species (*A. cornuta* and *A. bonnevieae*) do not correspond readily to any of the described genera in the tribe Cladocarpini Calder, 1997a, and a case could be made for a new genus to accommodate these two. For now, however, we have taken a conservative approach and have retained them in *Aglaophenopsis*.

In *Cladocarpus formosus*, type species of the genus, the mesial nematotheca on thecate internodes is almost entirely adnate to the abcaulinar wall of the hydrotheca except on the first internode, where there is a distinct gap between distal end of nematotheca and hydrothecal base (Figure 4F). Phylactocarps arise from this area. The same morphology is seen in *Cladocarpus integer* (Figure 5E, F) and *Cladocarpus diana*, with the mesial nematotheca being in a different position on the first thecate internode than on the others. In *C. diana*, however, the gap is not so apparent, with the phylactocarp arising clearly from the lateral side (Figure 3E). In *Aglaophenopsis cornuta*, the mesial nematotheca of the first cormidium is adnate to the hydrotheca, but it is displaced to the side as seen in frontal view. In all four of these species, the position of the mesial nematotheca with respect to the hydrotheca is different on the proximalmost internode of the hydrocladium than on the rest. In *Nematocarpus ramuliferus*, however, there is no such difference. Phylactocarps occur only on the first thecate internode in *Cladocarpus* s.l., and a gap exists between the mesial nematotheca and hydrotheca on this internode, even in species having nematothecae that are adnate to hydrothecae on other hydrocladial internodes. This difference also occurs in sterile colonies.

Gonothecae in *A. cornuta* and *C. formosus* occur on both apophyses (1–2 gonothecae) and on the phylactocarp. In *C. diana*, they arise from the phylactocarp. Gonothecae in hydroids of *C. integer* examined here were borne on the phylactocarp, although colonies with gonothecae on the stem, but lacking phylactocarps, are known in the species (Broch 1918). In *N. ramuliferus*, gonothecae occur only on apophyses of the main tube. Notably, colonies of *A. cornuta* and *C. formosus* with gonothecae, but with no phylactocarps, were observed in our material. Such colonies have also been reported in *Cladocarpus campanulatus* Ritchie, 1912 (Schuchert 2001). This suggests that the absence of phylactocarps in fertile material is probably much more common within the Cladocarpini than previously thought.

The most abundant species in our collections was *C. formosus*. *Cladocarpus integer* was found at the shallowest depth (119 m), while the deepest recorded species were *A. cornuta* and *C. formosus* (1885 m). The latter two species also had the widest bathymetric range (1645 m).

**TABLE 12.** Station data. GB, Grand Banks; FC, Flemish Cap; FP, Flemish Pass. T, bottom trawl; RD, rock dredge; SG, scallop gear. \*) Beothuk Knoll, SE Flemish Cap.

Zone	Station Code	Sam- pling gear	Date	Coordinates		Depth (m)		Species composition
				Start	End	Start	End	
Groundfish bottom trawl surveys								
FP	FN3L06 L44	T	08/08/2006	47°05.65N-46°50.98W	47°07.10N-46°50.84W	1185	1180	<i>Cladocarpus formosus</i>
FP	FN3L06 L51	T	09/08/2006	47°14.66N-47°33.01W	47°13.58N-47°31.45W	240	247	<i>Aglaophenopsis cornuta</i> , <i>C. formosus</i> , <i>Cladocarpus integer</i>
FP	FN3L06 L85	T	15/08/2006	46°19.64N-47°15.99W	46°21.03N-47°15.36W	498	493	<i>A. cornuta</i> , <i>C. formosus</i>
FP	FN3L06 L86	T	15/08/2006	46°18.85N-47°13.31W	46°21.18N-47°13.01W	617	610	<i>C. integer</i>
FP	FN3L06 L88	T	16/08/2006	46°45.09N-46°57.37W	46°46.54N-46°57.36W	1225	1218	<i>A. cornuta</i>
FP	FN3L06 L92	T	17/08/2006	46°37.81N-47°00.65W	46°36.55N-46°59.44W	1233	1242	<i>A. cornuta</i>
GB	PLA07 L61	T	11/06/2007	43°05.86N-49°29.92W	43°07.29N-49°29.60W	629	656	<i>A. cornuta</i> , <i>C. integer</i>
GB	PLA07 L70	T	12/06/2007	43°20.26N-49°14.37W	43°21.57N-49°13.52W	640	656	<i>C. formosus</i>
GB	PLA07 L73	T	13/06/2007	43°28.84N-49°29.29W	43°30.20N-49°25.19W	119	126	<i>C. integer</i>
GB	PLA07 L75	T	13/06/2007	43°38.67N-49°18.75W	43°39.57N-49°19.92W	450	368	<i>C. integer</i>
GB	PLA07 L76	T	13/06/2007	43°51.87N-49°10.30W	43°53.39N-49°10.24W	177	162	<i>C. integer</i>
GB	PLA07 L77	T	14/06/2007	43°43.88N-49°00.06W	43°45.49N-48°59.05W	620	575	<i>C. integer</i>
GB	PLA07 L78	T	14/06/2007	43°50.36N-49°02.23W	43°51.94N-49°02.21W	320	306	<i>C. integer</i>
GB	PLA07 L80	T	14/06/2007	44°03.10N-49°03.45W	44°01.39N-49°03.17W	300	317	<i>C. integer</i>
GB	PLA07 L86	T	15/06/2007	44°36.79N-48°57.22W	44°38.19N-48°57.44W	1000	996	<i>C. formosus</i>
GB	PLA07 L87	T	15/06/2007	44°45.67N-48°56.38W	44°47.06N-48°56.29W	1120	1160	<i>C. formosus</i>
GB	PLA07 L93	T	17/06/2007	45°24.90N-48°21.28W	45°23.83N-48°22.77W	1249	1266	<i>C. formosus</i>
GB	PLA07 L99	T	17/06/2007	45°36.54N-48°01.29W	45°37.41N-47°59.43W	1177	1158	<i>A. cornuta</i>
GB	PLA07 L101	T	18/06/2007	45°36.26N-47°50.56W	45°34.87N-47°50.48W	1374	1372	<i>C. formosus</i>
GB	PLA07 L107	T	19/06/2007	45°46.07N-47°59.75W	45°44.91N-48°01.33W	460	478	<i>A. cornuta</i>
FC	FC07 L21	T	25/06/2007	46°34.16N-46°09.96W	46°33.10N-46°08.11W	406	412	<i>C. formosus</i>
FC	FC07 L23	T	26/06/2007	46°21.90N-45°59.81W	46°21.07N-45°57.68W	527	542	<i>C. formosus</i> , <i>C. integer</i>
FC	FC07 L74	T	03/07/2007	48°13.60N-44°43.85W	48°14.76N-44°45.77W	596	599	<i>A. cornuta</i>

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TABLE 12. (Continued)

Zone	Station Code	Sam- pling gear	Date	Coordinates		Depth (m)		Species composition
				Start	End	Start	End	
FC	FC07 L123	T	09/07/2007	48°17.51N-45°45.05W	48°16.03N-45°46.14W	957	947	<i>C. integer</i>
FC	FC07 L133	T	11/07/2007	48°20.40N-44°25.22W	48°19.35N-44°23.37W	984	980	<i>A. cornuta</i>
FC	FC07 L153	T	14/07/2007	48°11.98N-45°52.97W	48°13.16N-45°51.41W	973	973	<i>A. cornuta</i>
FC	FC07 L155	T	15/07/2007	48°07.20N-46°11.60W	48°06.07N-46°13.14W	1186	1188	<i>C. formosus</i>
FC	FC07 L165	T	17/07/2007	46°59.28N-43°27.64W	47°57.60N-43°27.61W	1079	1078	<i>Cladocarpus diana</i>
FC	FC07 L166	T	17/07/2007	46°53.22N-43°23.48W	46°52.03N-43°25.11W	1242	1245	<i>C. formosus</i>
FC	FC07 L167	T	17/07/2007	46°51.46N-43°23.75W	46°50.65N-43°25.70W	1351	1381	<i>C. formosus</i>
FC	FC07 L169	T	18/07/2007	46°12.14N-45°36.00W	46°11.57N-45°38.22W	1216	1196	<i>C. diana</i>
FC	FC07 L171	T	18/07/2007	46°13.93N-45°54.56W	46°13.66N-45°57.00W	874	838	<i>A. cornuta, C. diana, C. formosus</i>
FC	FC07 L177	T	19/07/2007	46°56.46N-46°40.21W	46°58.02N-46°39.20W	770	797	<i>A. cornuta</i>
FC	FC07 L178	T	19/07/2007	47°06.18N-46°37.13W	47°07.76N-46°36.66W	866	878	<i>A. cornuta</i>
FP	FN3L08 L66	T	04/08/2008	46°52.67N-47°07.71W	46°51.24N-47°07.80W	1026	1016	<i>C. formosus</i>
FP	FN3L08 L88	T	09/08/2008	46°02.71N-47°24.69W	46°01.84N-47°26.36W	1198	1185	<i>A. cornuta, C. formosus</i>
FP	FN3L08 L89	T	09/08/2008	46°03.72N-47°37.38W	46°02.57N-47°38.70W	392	392	<i>A. cornuta</i>
FP	FN3L09 L80	T	08/08/2009	46°14.05N-47°23.78W	46°12.97N-47°25.32W	426	425	<i>A. cornuta, C. integer</i>
FP	FN3L09 L88	T	10/08/2009	46°14.04N-46°59.34W	46°12.56N-46°59.74W	1386	1399	<i>C. formosus</i>
FP	FN3L09 L89	T	10/08/2009	46°06.06N-47°20.00W	46°07.45N-47°18.22W	1005	975	<i>A. cornuta</i>
FP	FN3L10 L35	T	01/08/2010	47°41.49N-47°12.39W	47°40.03N-47°13.03W	362	345	<i>A. cornuta, C. formosus</i>
FP	FN3L10 L57	T	05/08/2010	46°57.46N-47°15.95W	46°58.94N-47°16.27W	462	456	<i>A. cornuta</i>
FP	FN3L10 L87	T	11/08/2010	46°09.97N-47°21.40W	46°10.81N-47°19.78W	731	661	<i>A. cornuta</i>
NEREIDA surveys								
FC	NEREIDA0509 RD4	RD	31/05/2009	48°28.47N-44°07.37W	48°28.76N-44°06.84W	1852	1853	<i>A. cornuta, C. formosus</i>
FC	NEREIDA0509 RD6	RD	01/06/2009	48°17.49N-44°03.65W	48°17.13N-44°03.52W	1348	1321	<i>A. cornuta, C. formosus</i>
FC	NEREIDA0509 RD7	RD	02/06/2009	48°15.38N-44°01.85W	48°13.93N-43°59.56W	1339	1319	<i>A. cornuta, C. integer</i>
FC	NEREIDA0509 RD9	RD	04/06/2009	48°05.69N-44°08.76W	48°05.29N-44°08.27W	864	861	<i>C. integer</i>
FC	NEREIDA0509 RD10	RD	05/06/2009	48°00.03N-43°45.64W	48°00.54N-43°45.65W	1554	1607	<i>C. formosus</i>

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TABLE 12. (Continued)

Zone	Station Code	Sam- pling gear	Date	Coordinates		Depth (m)		Species composition
				Start	End	Start	End	
FC	NEREIDA0509 RD12	RD	06/06/2009	47°46.63N-43°34.49W	47°47.00N-43°34.88W	1462	1453	<i>C. formosus</i>
FC	NEREIDA0509 RD15	RD	08/06/2009	47°33.22N-43°32.03W	47°33.40N-43°32.35W	1358	1342	<i>C. diana, C. formosus</i>
FC	NEREIDA0509 RD18	SG	13/06/2009	47°15.71N-43°31.86W	47°15.60N-43°32.01W	1079	1071	<i>C. diana, C. formosus</i>
FC	NEREIDA0509 RD19	SG	14/06/2009	47°09.86N-43°28.58W	47°09.95N-43°28.69W	1137	1132	<i>C. formosus</i>
FC	NEREIDA0509 RD20	SG	15/06/2009	47°04.33N-43°26.95W	47°04.25N-43°27.10W	1122	1113	<i>C. diana, C. formosus</i>
FC	NEREIDA0509 RD21	SG	16/06/2009	46°50.76N-43°43.06W	46°50.74N-43°43.31W	870	871	<i>C. formosus</i>
FC	NEREIDA0509 RD22	SG	17/06/2009	46°50.40N-43°38.42W	46°50.53N-43°38.54W	956	943	<i>C. formosus</i>
FC	NEREIDA0509 RD23	SG	18/06/2009	46°46.49N-43°51.91W	46°46.43N-43°52.18W	1127	1108	<i>C. formosus</i>
FC	NEREIDA0509 RD24	SG	19/06/2009	46°41.65N-43°58.12W	46°41.53N-43°58.26W	1104	1112	<i>C. formosus</i>
FP	NEREIDA0609 RD26	RD	27/06/2009	48°13.50N-47°31.43W	48°13.29N-47°31.17W	1575	1584	<i>A. cornuta</i>
FP	NEREIDA0609 RD27	RD	28/06/2009	48°07.41N-47°06.00W	48°07.39N-47°06.32W	846	859	<i>A. cornuta, C. formosus, Nematocarpus ramuliferus</i>
FP	NEREIDA0609 RD28	RD	28/06/2009	48°09.34N-46°49.92W	48°09.13N-46°49.70W	794	801	<i>A. cornuta, C. formosus</i>
FC	NEREIDA0609 RD36	RD	07/07/2009	48°24.26N-45°42.21W	48°24.35N-45°41.73W	1005	991	<i>C. diana</i>
FC	NEREIDA0609 RD38	RD	10/07/2009	48°59.71N-45°14.28W	48°59.59N-45°13.84W	1575	1561	<i>C. diana</i>
FC	NEREIDA0609 RD41	RD	13/07/2009	49°00.87N-44°48.09W	49°00.90N-44°48.44W	1885	1879	<i>A. cornuta, C. formosus</i>
FP	NEREIDA0709 RD49	RD	13/08/2009	47°02.42N-47°11.33W	47°02.72N-47°11.31W	780	778	<i>A. cornuta, C. formosus</i>
FP	NEREIDA0709 RD51	RD	14/08/2009	46°48.55N-46°56.90W	46°48.31N-46°56.96W	1216	1215	<i>C. formosus</i>
FP	NEREIDA0709 RD57	RD	19/08/2009	46°37.35N-46°54.31W	46°37.38N-46°54.01W	1248	1252	<i>C. formosus</i>
FP	NEREIDA0709 RD59	RD	20/08/2009	46°23.69N-46°58.27W	46°23.38N-46°58.25W	768	795	<i>A. cornuta, C. formosus</i>
FP	NEREIDA0709 RD60	RD	20/08/2009	46°18.10N-46°56.81W	46°18.67N-46°56.19W	726	712	<i>A. cornuta</i>
FC	NEREIDA0610 RD62	RD	13/06/2010	46°21.90N-46°05.28W	46°22.26N-46°05.37W	631	605	<i>A. cornuta, C. diana, C. formosus, C. integer, N. ramuliferus</i>
FC	NEREIDA0610 RD63	RD	14/06/2010	46°22.18N-44°59.67W	46°22.17N-45°00.17W	1406	1486	<i>C. diana, C. formosus</i>
FC	NEREIDA0610 RD64	RD	15/06/2010	46°25.43N-44°50.75W	46°25.73N-44°50.75W	1091	998	<i>C. diana, C. formosus, N. ramuliferus</i>
FC	NEREIDA0610 RD65	RD	18/06/2010	46°07.38N-45°50.16W	46°07.43N-45°50.61W	1589	1484	<i>C. formosus</i>
FC	NEREIDA0610 RD66	RD	21/06/2010	46°25.41N-45°21.27W	46°25.68N-45°21.57W	818	672	<i>C. formosus</i>

.....continued on the next page

TABLE 12. (Continued)

Zone	Station Code	Sam- pling gear	Date	Coordinates		Depth (m)		Species composition
				Start	End	Start	End	
FC	NEREIDA0610 RD67*	RD	23/06/2010	46°16.06N-46°32.57W	46°15.82N-46°32.70W	613	600	<i>A. cornuta</i> , <i>C. diana</i> , <i>C. formosus</i> , <i>C. integer</i>
FC	NEREIDA0610 RD71*	RD	27/06/2010	46°04.80N-46°20.52W	46°05.15N-46°20.82W	888	784	<i>A. cornuta</i> , <i>C. diana</i> , <i>C. formosus</i>
FP	NEREIDA0610 RD74	RD	30/06/2010	46°15.11N-46°55.17W	46°15.27N-46°55.45W	1055	990	<i>A. cornuta</i> , <i>C. formosus</i> , <i>N. ramuliferus</i>
FC	NEREIDA0710 RD75*	RD	06/07/2010	45°52.15N-46°49.26W	45°52.57N-46°48.75W	1227	1150	<i>A. cornuta</i>
FP	NEREIDA0710 RD76	RD	07/07/2010	46°12.14N-46°57.67W	46°12.38N-46°57.07W	1294	1353	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0710 RD77	RD	08/07/2010	46°03.75N-47°32.47W	46°04.25N-47°32.47W	697	707	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0710 RD78	RD	09/07/2010	45°54.44N-47°42.25W	45°54.16N-47°42.87W	749	745	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0710 RD79	RD	10/07/2010	45°52.00N-47°36.77W	45°52.36N-47°36.20W	1134	1152	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0710 RD80	RD	11/07/2010	45°51.33N-47°47.78W	45°51.67N-47°48.41W	699	619	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i>
GB	NEREIDA0710 RD83	RD	14/07/2010	45°34.09N-48°07.05W	45°34.42N-48°07.61W	1043	997	<i>C. formosus</i>
GB	NEREIDA0710 RD85	RD	16/07/2010	45°23.53N-48°32.91W	45°23.22N-48°33.40W	592	631	<i>C. formosus</i>
GB	NEREIDA0710 RD86	RD	17/07/2010	45°22.13N-48°35.61W	45°22.58N-48°35.30W	1263	1231	<i>C. formosus</i>
GB	NEREIDA0710 RD87	RD	18/07/2010	45°24.26N-48°34.41W	45°24.60N-48°34.08W	604	512	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i>
GB	NEREIDA0710 RD88	RD	19/07/2010	45°22.35N-48°34.05W	45°22.07N-48°33.58W	676	700	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i> , <i>N. ramuliferus</i>
GB	NEREIDA0710 RD89	RD	20/07/2010	45°20.13N-48°34.82W	45°19.64N-48°34.64W	1135	1280	<i>C. integer</i>
GB	NEREIDA0710 RD92	RD	23/07/2010	44°34.94N-48°58.34W	44°34.75N-48°57.63W	773	890	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0710 RD95	RD	26/07/2010	43°43.96N-48°58.41W	43°44.42N-48°58.65W	898	810	<i>C. formosus</i>
GB	NEREIDA0810 RD97	RD	01/08/2010	43°44.59N-48°59.09W	43°44.93N-48°58.61W	740	802	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i>
GB	NEREIDA0810 RD98	RD	02/08/2010	43°26.09N-49°05.54W	43°26.29N-49°06.12W	1038	1100	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i>
GB	NEREIDA0810 RD99	RD	03/08/2010	43°36.88N-49°04.69W	43°37.33N-49°04.83W	548	520	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i>
GB	NEREIDA0810 RD100	RD	04/08/2010	43°29.06N-49°11.13W	43°29.40N-49°10.73W	694	587	<i>A. cornuta</i> , <i>C. formosus</i> , <i>C. integer</i>
GB	NEREIDA0810 RD101	RD	05/08/2010	43°17.37N-49°12.88W	43°17.78N-49°12.68W	875	894	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0810 RD102	RD	07/08/2010	43°06.26N-49°24.75W	43°06.61N-49°24.35W	654	698	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0810 RD103	RD	10/08/2010	42°56.60N-49°33.73W	42°56.88N-49°33.19W	1154	1177	<i>A. cornuta</i> , <i>C. formosus</i>
GB	NEREIDA0810 RD104	RD	11/08/2010	42°56.32N-49°33.71W	42°56.79N-49°33.45W	1190	1137	<i>A. cornuta</i> , <i>C. formosus</i>



Hydroids of exceptionally large size were collected in some of the species (Table 9). The largest colony, a specimen of *C. integer*, was 78.0 cm high. The largest ones of *C. formosus* and *A. cornuta* were 53.5 cm and 28.7 cm high, respectively. *Cladocarpus diana* and *N. ramuliferus* are small hydroids not exceeding 7.0 cm in height.

Of particular research interest, the habitat provided by several deep-water anthozoans has been emphasized only recently. The question arises whether large hydroid colonies, such as those found here, might also provide important substrate and shelter. However, sessile epibionts and vagile invertebrates were scarce amongst the colonies examined. Observed associates included other hydroids, alcyoniids, brachiopods, barnacles, bryozoans, and caprellid amphipods. Such a limited number of associates suggests that these hydroids may have effective antifouling defenses.

## Identification key to aglaopheniid hydroids reported from the western North Atlantic between 40°N and Baffin Bay, including western Greenland

- 1 Gonothecae protected by a closed corbula formed by modified hydrocladia bearing nematothecae and hydrothecae ..... *Lytocarpia myriophyllum*
- Gonothecae solitary, protected by unbranched or branched phylactocarps or unprotected ..... 2
- 2 Colonies with a segmented appendage having nematothecae (ramulus) that arches over the hydrothecae on abaxial side of most hydrocladial internodes; aperture of hydrothecae strongly tilted towards abaxial side ..... *Nematocarpus ramuliferus*
- Colonies with or without a segmented appendage having nematothecae (phylactocarps) only on first proximal thecate internode (fertile specimens); aperture of hydrothecae not strongly tilted towards abcauline side ..... 3
- 3 Phylactocarp strongly septate, forked (Y-shaped) or alternately branched (without secondary branching), with 1–2 terminal hydrothecae or having a series of hydrothecae ..... 4
- Phylactocarp not strongly septate, unbranched or dichotomously branched (antler-shaped), sometimes also with secondary branching, without hydrothecae ..... 6
- 4 Hydrothecae with a strong and pointed median keel of perisarc arising above mesial nematotheca, largely surpassing level of hydrothecal rim; mesial nematotheca large, extending 1/3–1/2 up hydrotheca ..... 5
- No median keel present; mesial nematotheca short, separate from hydrotheca or only slightly adnate to it ..... *Aglaophenopsis verrilli*
- 5 Hydrotheca cone-shaped, notably wider distally, with no intrathecal septum; hydrothecal rim cusped; phylactocarp forked (Y-shaped) with one terminal hydrotheca on each branch. .... *Aglaophenopsis cornuta*
- Hydrotheca of uniform width, with an intrathecal septum; hydrothecal rim slightly crenulated; phylactocarp alternately branched, each branch with a series of hydrothecae. .... *Aglaophenopsis bonneviesae* (SW Greenland)
- 6 Hydrothecae bulging deeply into lumen of hydrocladium; hydrothecal rim even; phylactocarp unbranched, sometimes absent in fertile colonies. .... *Cladocarpus integer*
- Hydrothecae not bulging deeply into lumen of hydrocladium; hydrothecal rim undulated to decidedly cusped; phylactocarp branched; if unbranched, hydrothecae campanulate ..... 7
- 7 Hydrothecal rim with deep cusps; mesial nematothecae on thecate internodes very broad, sometimes notched in middle, not tapering distally in front view, with a wide aperture and distal end extending only 1/10–1/11 along hydrotheca. .... *Cladocarpus diana*
- Hydrothecal rim undulated or with shallow cusps; mesial nematothecae not as above ..... 8
- 8 Mesial nematotheca extending 1/2–4/5 up hydrotheca; hydrotheca normally with two slightly prominent mesial outer cusps on abcauline side; intrathecal septum short to well developed, arising from abcauline wall of hydrotheca, frequently curved backwards; mature gonotheca forming a distinct hood overarching the opening; aperture lateral, narrowly oval ..... *Cladocarpus formosus*
- Mesial nematotheca free from hydrotheca or only reaching hydrothecal base; hydrotheca with or without one abcauline cusp; intrathecal septum not well formed or absent, although an annular ridge along hydrothecal wall may occur; gonotheca without a hood; aperture terminal or subterminal, broadly oval ..... 9
- 9 Hydrothecae campanulate, with annular ridge at lower third; mesial nematotheca reaching hydrothecal base, opening into lumen of segment at adcauline side; phylactocarp poorly developed, unbranched ..... *Cladocarpus campanulatus* (SW Greenland)
- Hydrothecae elongate, rather distant, with no intrathecal septum; characteristic strong median abcauline cusp; mesial inferior nematotheca free from hydrotheca or nearly so, not opening into lumen; phylactocarp well developed, dichotomously branched, antler-shaped. .... *Cladocarpus flexilis*

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